Springs as models to unveil ecological drivers and responses: Perspectives for ecosystem theory from neglected ecosystems

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"*Es gibt nichts Praktischeres als eine gute Theorie.*"

(Nothing is as practical as a good theory)

Immanuel Kant

Contents

1 Introduction

1.1 My motivation and theoretical background for this thesis

> *"It is important to define the central goal of ecological research before discussing how such work should be done"* David Tilman (1989, p. 136).

The improvement of understanding is the general goal of science (Kuhn 1962, Picket et al. 2007). The primary objective in ecology is to understand "the processes influencing the distribution and abundance of organisms, the interaction among organisms, and the interaction between organisms and the transformation and flux of energy and matter" (Likens 1992). This broad definition of ecology as a scientific discipline integrates two major perspectives, the organismal as well as the systemic perspective. Whereas the organismal perspective has a strong focus on processes acting among single organisms or species (thus system elements) (Morin 2011) the systemic perspective strongly focuses on the distribution and fluxes of material, energy and information regulated by ecosystems (Margalef 1975, Abel 1998, Beierkuhnlein 2007).

Another general goal of science is consilience, meaning the synthesis of knowledge (Wilson 1998, Grace 2015). Ecology as scientific discipline has a rather broad focus which would in principle favour the integration of knowledge. However, ecological research often appears as a series of case studies in isolated sub-disciplines with loose relation to each other (Picket et al. 2007). Among all disciplines of science, biology (including ecology) is the fastest evolving science of the last two centuries (Collins 2011). Concomitant with this fast development of ecology, numerous sub-disciplines with differing perspectives, concepts and theories have emerged (McIntosh 1987, Kolasa 2011). This increasing divergence during the development of ecology led amongst others to community ecology, dealing with the interaction of organisms without considering system aspects (fluxes of information, energy and matter in systems) and systems ecology, focusing on the systems perspective but ignoring the idiosyncrasies at the organismic level (Picket et al. 2007). This divergence into sub-disciplines increases detailed understanding in the particular sub-disciplines of ecology but at the same time diminishes scientific progress towards general concepts (Marquet et al. 2014). Scientific progress leading to the overall understanding about the processes which maintains the functioning of complex ecological systems is a prerequisite when we want to pursue consilience in ecology.

Although the divergence of ecology in different sub-disciplines might be a natural process related to the evolution of systems, a general, integrative understanding of ecosystem functioning is nowadays more topical than ever. Ongoing anthropogenic intervention changes ecosystem functioning and, thus, service provisioning. However, predictions about these changes, which are a prerequisite to counteract these developments, lack in generality and, thus, are characterized by high uncertainty. This high uncertainty of predictions, which impedes concrete proposals to counterbalance negative developments, can be reduced

by increasing generality in ecological understanding. When aiming for an integrative ecological understanding, combining organismal and systemic perspectives is assumed to open promising perspectives towards a truly integrative ecology (Picket et al. 2007). Already Brown (1995) suggested that community ecology and systems ecology need to be brought together. In this thesis I want to pursue this philosophy by integrating the two perspectives conceptualized in community and systems ecology.

The technological progress during the last decades (e.g. next generation sequencing, high resolution remote sensing via satellites, increasing computational power) increased our ability to collect and analyse ecological data across large spatial, temporal and organismal scales. This vast amount of data, however, generates new challenges for ecology as a scientific discipline (Marquet et al. 2014). Proper theoretical frameworks are needed to prevent ecology from "drowning in [this] sea of data" (Brenner 2012, p. 461). An integrative theory is, thus, a prerequisite when aiming for a comprehensive understanding of ecological processes and patterns (Picket el al. 2007, Scheiner & Willig 2011). Searching for such kind of integrative theory, I decided to use the theory of complex adaptive systems as a theoretical framework for my thesis. The theory of complex adaptive systems is proposed as a general theory describing the functioning of complex systems including ecosystems (Levin 1992, Gell-Mann 1994). For ecological systems this general theory integrates the perspectives of traditional community ecology and systems ecology (Brown 1995). In a complex adaptive systems perspective, ecological systems are seen as complex assemblages of biotic elements (e.g. cells, organisms, species, communities) which interact with each other and with the abiotic environment in which they are embedded, across a multitude of spatial, temporal and organisational scales (Levin 1992, Hartvigsen et al. 1998). A detailed description of this theoretical concept is given in later chapters of the introduction (Chapter 1.6).

The applicability of complex adaptive systems theory has been discussed for several ecological systems including colonies of social insects (Bonabeau 1998), rangelands (Gross et al. 2006) and forests (Messier et al. 2013). Furthermore, this holistic theoretical concept has been shown to be applicable beyond ecology, including the evolution of technology (Flemming & Sorenson 2001), society (Buckley 2008) and language (Beckner et al. 2009), economics (Choi et al. 2001) and health care (Rouse 2008). The integrative and transdisciplinary character of the complex adaptive systems theory might therefore help to increase the interplay and integration of different ecological sub-disciplines or even scientific disciplines. However, a general, exhaustive test of this theory is missing so far. With the test of the complex adaptive systems theory for one model ecosystem, namely springs, I want to contribute to a more integrative understanding of ecological systems.

Springs in general but especially seepage springs ('Helokrene' sensu Thienemann 1924), which can be found in a high spatial density in the lower mountain ranges of Central Germany are ideal model ecosystems for a detailed test of the complex adaptive systems theory for ecological systems (see Chapter 1.3). The experiment-like setting provided by springs as water dependent ecosystems was already realized by the renowned ecologist Eugene Odum, who described springs as "natural constant temperature laboratories" which "hold a position of importance as study areas that is out of proportion to their size and number" (Odum 1971). The long-term study of numerous of these springs on landscape scale, which is the basis of this thesis, allows for a rigorous testing of general theories like the complex adaptive systems

theory in an experiment-like, ‘controlled’ setting under close-to-natural-conditions which yield more realistic results compared to artificial settings of controlled but ‘man-made’ ecological experiments (c.f. Beierkuhnlein 1994, see Chapter 1.3.2 for more details).

In this thesis I give a strong emphasis on general aspects of science like the generation and integration of understanding embedded in the rather general theoretical framework of the complex adaptive systems theory. This seems to be quite distant from the ecological issues, which are relevant for the practice related to nature conservation or climate change assessments. However, integrative ecological theory and its rigorous testing is a prerequisite to stimulate advances in environmental science which are urgently needed to develop sound adaptation and mitigation strategies in our rapidly changing world (Collins 2011, White et al. 2010, Guisan & Rahbek 2011). Aiming for integration in ecology will, thus, not only improve the progress of basic ecological science but will also enhance the effectiveness of applied environmental science (Picket et al. 2007).

1.2 Structure of this thesis

With this dissertation I want to synthesize two major ecological sub-disciplines with quite different perspectives, namely community ecology and systems ecology into the general, theoretical framework of complex adaptive systems theory. By applying this holistic theory on spring ecosystems as natural experiments with controllable settings I want to contribute to enhanced interdisciplinarity in ecological science, a trait which lost attention during the last decades of ecological research that were characterised by increasing specialisation of ecology and the increasing focus on details within its sub-disciplines (Kolasa 2011).

I will start with sketching the existing knowledge and understanding of spring ecosystems before I will introduce the seepage spring ecosystems studied in this dissertation and discuss their potential as ideal model ecosystems to test general ecological theories. Furthermore, I will give a short excursus about the potentials and challenges related to different types of model ecosystems ranging from fully controllable but artificial systems (e.g. Ecotron, Lawton 1995) to natural but very complex model ecosystems like Barro Colorado Island (Leigh Jr 1999) or the springs studied in this thesis.

A sound theoretical framework is the backbone of empirical research. However, current trends in ecology suggest an increasing focus on empirical research concomitant with a decrease in theoretical considerations (NRC 2008, Marquet et al. 2014). In the light of this current development in ecological research I will furthermore outline the different theoretical approaches used in ecology (reductionism vs. holism) in a historical and thematic context and discuss the pros and cons of ecological theory in its role to promote modern ecological research. Furthermore I will put the theory of complex adaptive systems into this general framework of ecological theory to examine the relevance of this rather holistic theory to understand current ecological problems and find potential solutions.

Complex adaptive systems theory is a quite general theoretical framework which needs to be concretized before an empirical examination can be applied to it. Therefore I will subdivide the general framework in five major principles which are stated by several authors to be relevant to develop a general picture of ecosystem functioning based on the complex adaptive systems theory (Margalef 1975, Gell-Mann 1994, Brown 1997, Levin 1998, Levin 2002, Filotas et al. 2014). Major principles are here defined as broad, theoretical statements, which describe observable patterns and underlying processes that sufficiently describe the propositions of the general theory to allow empirical tests (c.f. Scheiner & Willig 2008). All of the five major principles were empirically examined in this thesis for seepage springs in the lower mountain ranges of Central Germany by at least one manuscript:

1) Diversity and organisation of biotic system elements, particularly spatial patterns of plant community structure (species diversity, commonness and rarity, **Manuscript 1**).

2) Flow, distribution and interaction of information, energy and matter, meaning the major abiotic environmental drivers of biotic responses and the interactions among these drivers and between the abiotic drivers and the biotic system elements, i.e. plant species (**Manuscript 1, 2, 3 and 5**).

3) Stability and non-linearity of system reaction, meaning the response characteristics of biotic elements related to abiotic drivers (species and community stability, **Manuscript 2**).

4) Scale-dependence and cross-scale similarity of system properties (e.g. species realised temperature niches, **Manuscript 5**).

5) Path-dependence of the system, in particular the effect of historic environmental stressors (i.e. atmospheric acidification during the 1960s to 1980s) on current community responses in interaction with current environmental changes (extreme drought events: **Manuscript 2** and road salt application during winter: **Manuscript 3**) and species, which actively change environmental conditions (ecosystem engineers, **Manuscript 4**).

The importance of this integrative approach to look at ecosystems have been already recognized but coherent and rigorous tests for the underlying assumptions are widely missing (see also Hartvigsen et al. 1998). By testing the theory of complex adaptive systems and its major principles for one type of ecosystem, namely seepage springs, this thesis provides a first comprehensive picture of an important theoretical framework in current ecological science.

For each of the five major principles the theoretical background as well as the current state of empirical research will be discussed in the subsequent sections of the introduction. Finally, I give practical advice on methodological requirements for testing and further developing the theoretical framework of complex adaptive systems in ecology, in particular the role of long-term monitoring in order to cover the temporal dimensions of causes and ecological effects and the role of an adequate sampling design in order to cover the spatial scales and dimensions of the investigated processes (**Manuscript 6**).

Box 1: Definitions and explanations of concepts and terms used in this dissertation.

Adaptation: Evidently, adaptation and complexity are the two major characteristics of complex adaptive systems. I here define adaptation as adjustment in the reaction and attributes of an ecological system as a response to changing environmental conditions (Filotas et al. 2014). In other words, adaptation is the evolving property of complex systems, which results from continuous interactions and feedbacks among biotic system elements (e.g. organisms or species) and the abiotic environment and therefore affects future interactions and feedbacks, thus, ecosystem functioning (Holland 1992, Gell-Mann 1994, Holland 2006). In contrast to direct adaptation (response characteristics are not changing through time), adaptation of complex systems includes system's learning from past circumstances and, thus, system's evolution (Holland 1992, Gell-Mann 1994). In other words, the reaction of complex systems like ecosystems to environmental triggers changes through time although the triggering environmental conditions might remain the same.

Complexity: Complexity as the second major property of complex adaptive systems describes the interconnectedness of the elements of a system. Due to the plethora of interconnections which characterize complex systems, they cannot be sufficiently described by the properties of its individual elements (Gallagher & Appenzeller 1999, Lenton & Oijen 2002).

Complex adaptive systems: Complex adaptive systems can be defined as a collectivity of adaptively interacting elements. Thus, diversity, individuality and organisation of the system elements, interactions between those elements and among elements and the environment across scales, non-linearity and stability in the system's reaction to changing environmental conditions and the dependency of those reactions on previous circumstances (path-dependence) play a major role in complex adaptive systems (Holland 1995, Levin 1998, Margaleff 1975, Gell-Mann 1994).

Ecological niche: Here I refer to Hutchinson's concept of the ecological niche who separates between the 1) fundamental ecological niche of a certain species, defined as a multi-dimensional space of environmental conditions under which a certain species would be able to exist and reproduce and 2) the realized ecological niche of a species which refers to the abiotic environmental conditions under which a certain species actually co-exists with other, co-occurring and, thus, interacting species (c.f. Hutchinson 1957).

Ecological monitoring: Ecological monitoring is discussed in this dissertation to be an important tool when studying the functioning of complex ecological systems. I here define ecological monitoring as the periodic recording of ecological features regarding their composition, structure and function through time, which can range from a single variable measured at a single location to a plethora of variables measured on a national scale (Hellawell 1991, Gitzen et al. 2012). The temporal period of monitoring and its sufficiency to capture important properties of complex adaptive systems like path-dependence is therefore strongly dependent on the speed of the adaptive cycles driving system evolution. The faster feedbacks between biotic system elements and the abiotic environment occur, the shorter the period of time a system has to be monitored to sufficiently capture the effects of ecosystem history on actual ecosystem functioning. The speed of feedback loops (adaptive cycles) thereby strongly goes along with the generation cycles of the interacting species.

Box 1 continued

Major principles: Major principles as important parts of general theories (like the complex adaptive systems theory, see definition of theory) are here defined as broad statements about empirical patterns and the processes that operate within a certain domain, which means a given class of phenomena in the natural world (Scheiner & Willig 2008, Scheiner & Willig 2011, Marquet et al. 2014).

Pattern: A pattern is here defined as a non-random signal which is caused by a process and forms a certain detectable structure on a certain scale of space, time or organismic association (c.f. Grimm et al. 2005).

Process: A process is a transformation event caused by the interaction of biotic system elements and / or abiotic environmental conditions.

Scale: Scale is defined as a unit of space, time or organismic association in terms of grain size and extent (c.f. Allen & Starr 1982; Turner et al. 2001). The extent thereby refers to the overall area covered by a particular study, whereas the grain size defines the size of the individual units of observation (Wiens 1989).

Statistical power: The statistical power is defined as 1-beta, where beta is the type II error rate of a statistical test, meaning the chance of a statistical test to miss a pattern which actually exists (Di Stefano 2003). The statistical power is therefore the probability of a statistical test to reject the null hypothesis (which assumes no effect) when it is false, means an effect exists (Osenberg et al. 1994).

Theory: In the broadest sense, a theory in ecology is an assembly of ideas to explain the functioning of the natural world (c.f. Marquet et al. 2014). Thus, "a theory is a way of looking at the world and not necessary a way of knowing how the world is." (Marquet et al. 2014, p. 3). In more technical terms, a theory is a hierarchical framework that connects major principles with highly specific models and testable hypotheses (Scheiner & Willig 2011). Depending on the scope of a theory, one can separate between general and constitutive theories. A general theory is thereby broad in scope subsuming several interrelated patterns and mechanisms whereas constitutive theories include more precise statements about a particular aspect within the general domain of the general theory (Scheiner & Willig 2008, 2011). Thereby general theories like the theory of complex adaptive systems subsume several constitutive theories like e.g. the ecological niche theory (Hutchinson 1957) or the theoretical concepts of hysteresis, stability and alternative stable states (Holling 1973, Beisner et al. 2003, see also Table 1). Constitutive theories can be thereby classified by referring them to major principles as important parts of a general theory (see above).

1.3 Springs as neglected model ecosystems

"*Ad fontes*" *(To the sources)* Guiding principle in Renaissance humanism

1.3.1 Current knowledge about springs

Springs are outstanding ecosystems because of their environmental and ecological coherence. This qualifies these semi-aquatic systems as ideal models that can be used to increase our understanding of complex ecosystems under experiment-like settings. Although most spring ecosystems are very small in size, they harbour high biodiversity and are exclusive habitats for many specialised species. Additionally, these isolated ecosystems and the specific properties they exhibit are globally distributed and partly abundant not only in humid climate because of their water supply from groundwater (Cantonati et al. 2012a, Glazier 2012). However, springs are completely underrepresented in ecological research (Cantonati et al. 2012a, b) and their potential to test and elaborate on ecological theories has been neglected so far.

In this chapter I will illustrate the current knowledge about the springs studied in this thesis. I will furthermore sketch the research landscape related to the research on springs in general during the last 26 years based on a literature survey I conducted. Afterwards I will discuss the potential of springs as ideal model ecosystems to study functioning of complex ecosystems and give a short excursus about the strengths and weaknesses of the different types of model ecosystems ranging between full control and full complexity.

In contrast to the general lack of knowledge about spring ecosystems, the helocrenic springs of the lower mountain ranges of Central Germany, which are the object of study in this dissertation, are intensively investigated and monitored since 1989 and, thus, have a long history of ecological research (c.f. Beierkuhnlein 1991, Beierkuhnlein 1994, Audorff 1997, Beierkuhnlein & Gollan 1999, Audorff 2009). Extensive phytosociological knowledge exists about the plant communities and detailed information is available about the physico-chemical characteristics of the spring waters (Beierkuhnlein & Durka 1993, Beierkuhnlein 1994, Beierkuhnlein et al. 1999, Audorff et al. 1999, Beierkuhnlein 1999, Beierkuhnlein & Schmidt 1999, Peintinger & Beierkunhnlein 1999, Riedel & Beierkuhnlein 1999). Detailed information exists about the hydrological (Lischeid 1999), hydrogeological (Kleber et al. 1998, Kleber & Schellenberger 1999), geomorphological (Beierkuhnlein & Kleber 1999), pedological (Dieffenbach et al. 1999) and atmospheric environmental conditions (temperature and radiation, Beierkuhnlein & Gräsle 1998, Gräsle & Beierkuhnlein 1999) characterising these springs and the related catchments. Nitrous and sulphuric atmospheric depositions, which peaked in the late 1980's in the studied region of Central Germany, were reported to change the biogeochemistry of the forested catchments and the water chemistry of the subsequent springs in terms of nutrients and acidification (Durka 1994, Durka

1999, Beierkuhnlein 1991, Beierkuhnlein & Durka 1993, Audorff & Beierkuhnlein 1999). Biogeochemical catchment traits like the acidity regime have been identified to indirectly affect plant species community composition via the physico-chemical properties of the outpouring groundwater (Strohbach et al. 2009, Audorff et al. 2011, Kapfer et al. 2012). In this thesis I use this solid basis of available information about the abiotic environmental conditions, the biotic elements of the systems (i.e. plant species) and the history (i.e. acidification) of these model ecosystems to get a general understanding about the different aspects of complex ecosystem functioning.

Springs are among the least studied aquatic ecosystems and almost completely underrepresented in ecological research despite their global importance for water supply and maintenance of biodiversity and, thus, ecosystem functioning and service provisioning like e.g. the supply with clean water (Cantonati et al. 2012a). To get an overview of the current knowledge about spring ecosystems I conducted a systematic literature survey using the Web of Science Database. The search was conducted on 10th of November 2015 at 3.15 PM by searching for: TITLE: ("springs" OR "crenic" OR "creno*") AND TOPIC: ("ecolo*" OR "biolo*"). The search was refined within the Web of Science Core Collection to the research area: ENVIRONMENTAL SCIENCES ECOLOGY in the research domain: SCIENCE TECHNOLOGY and a time period of 30 years (1985-2015). This search resulted in 541 articles from which 101 were excluded because of missing abstracts in the database and 60 studies were excluded as they examined different ecosystems (e.g. submarine springs or CO_2 springs). From the remaining 380 studies, which covered a temporal period of 26 years (1990 to 2015), titles and abstracts were screened to examine different aspects of research conducted on springs.

Most of the surveyed studies pursue clear ecological approaches (integrated studies of the abiotic environment and biotic system elements: 70.8%) whereas 16.6% have pure biological and 12.5% and pure abiotic focus. Almost half of the studies focus on micro-organisms (including bacteria, viruses and microalgae: 45.8%) followed by macroinvertebrates with 9.7% (Fig. 1A). Plants (including vascular plants and bryophytes), which are the biotic object of study in my thesis, are examined in only 5% of the studies and, thus, are visibly underrepresented in biological and ecological research conducted on springs (c.f. Cantonati et al. 2006, Spitale et al. 2012).

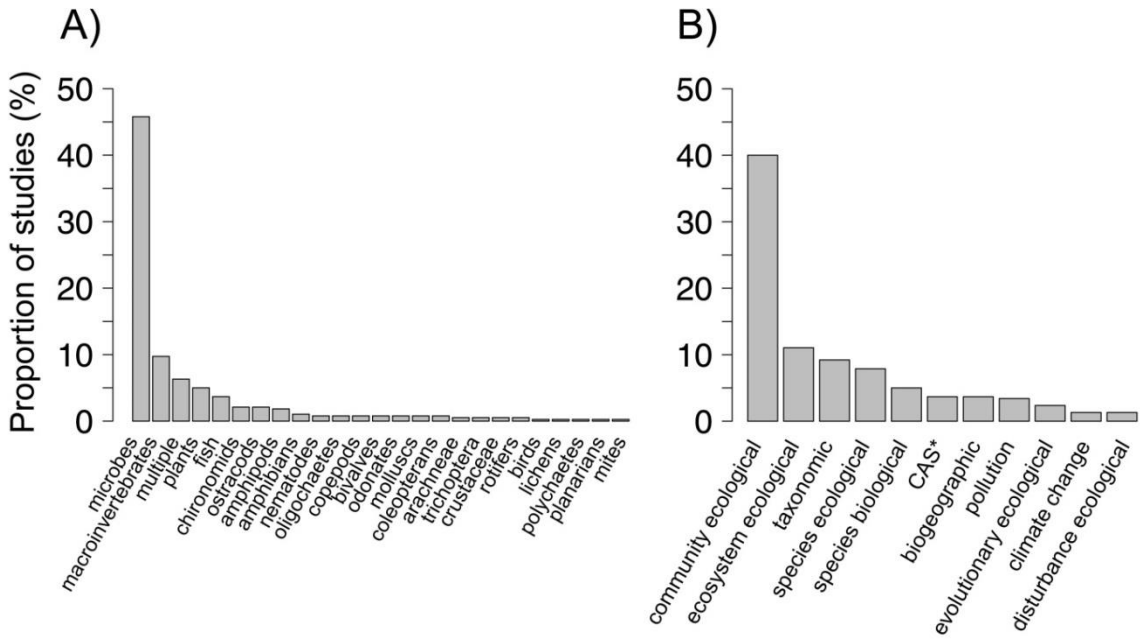

Figure 1: Organisms and thematic focus of studies conducted on springs during the last 26 years (1990-2015, n=380 studies); A) Studied organisms with microbes including bacteria, viruses and microalgae and plants including vascular plants and bryophytes (in 51 studies = 13.4% of all studies no organisms were studied or information about the studied organisms was missing in the title or abstract); B) Focus of the studies, CAS*: A complex adaptive systems (CAS) focus was assumed for studies which included at least two of the five major principles of the complex adaptive systems theory discussed in this dissertation (for 42 studies = 11.1% of all studies no particular focus was recognizable from the title or abstract).

Species community was the predominant organisational level examined in 60% of all studies followed by the species level with 25%. Multiple organisational levels were studied in 1.1% and the ecosystem level in 0.5% of all studies (in 51 studies = 13.4% no organisms were studied or information was not given in the title or abstract). Most studies had a community ecological focus (40% of all studies) followed by an ecosystem ecological perspective which was pursued in 11.1% of all studies (Fig. 1B). Taxonomic studies comprised 9.2% of all surveyed studies. Biogeographic studies focusing on the spatial pattern of species diversity across spatial scales are with 3.7% of all studies (14 studies) apparently less abundant. However, there are impressive studies such as Sekulova et al. (2012) which investigated species diversity of springs on continental scale. An equally minor amount of studies pursue a perspective related to complex adaptive systems theory. A complex adaptive systems perspective was assumed for a study when at least two of the five major principles discussed in this dissertation were addressed in the title or in the abstract of the publication. This criterion was met by 3.7% of all studies although none of these studies refers explicitly to the complex adaptive systems idea. Studies with a complex adaptive systems perspective are for example Keleher & Rader (2008) who examined the scale- and path-dependence of metaphyton community composition in the Bonneville Basin (Utah, USA) or the study of Sangiorgio et al. (2010) which tackles the effect of habitat size on spring ecosystem processes related to litter composition

by studying the interaction of habitat size, physico-chemical water properties, community structure of macroinvertebrates and rates of litter decomposition.

Overall, a strong emphasis in research is evident related to geothermal springs. Among the 37.6% of all surveyed studies on geothermal springs, 85.3% investigated microorganisms whereas the rest examined a variety of study organism including plants, birds, amphipods, molluscs, amphibians, macroinvertebrates, fish or dragonflies. This strong focus on microorganisms in geothermal springs can be explained by the fact that these extreme ecosystems and their inhabitants adapted to these specific conditions exhibit outstanding opportunities for research that cannot be found in other habitats. Studies of these communities are therefore relevant to understand the origin of life on earth and the potential of life on mars and exoplanets (Parenteau et al. 2014).

Although springs are mentioned by several authors to be ideal model ecosystems for ecological long-term monitoring (Cantonati et al. 2006, Cantonati et al. 2012a, Gerecke et al. 2011) a minor portion of the surveyed studies exceeded a study period of 10 years (7 studies equals 1.8% of all studies). Most studies were one-time investigations (67% of all studies, see Fig. 2A). Furthermore, most studies were conducted on a local (26.8%) or regional scale (58.4%), whereas only 7% of the studies examined larger spatial scales (Fig. 2B). Biomonitoring approaches were pursued in 9.5% of all studies (36 studies), whereas classifications of spring habitats (e.g. based on phytosociological criteria) were conducted in 10.3% of the studies (39 cases).

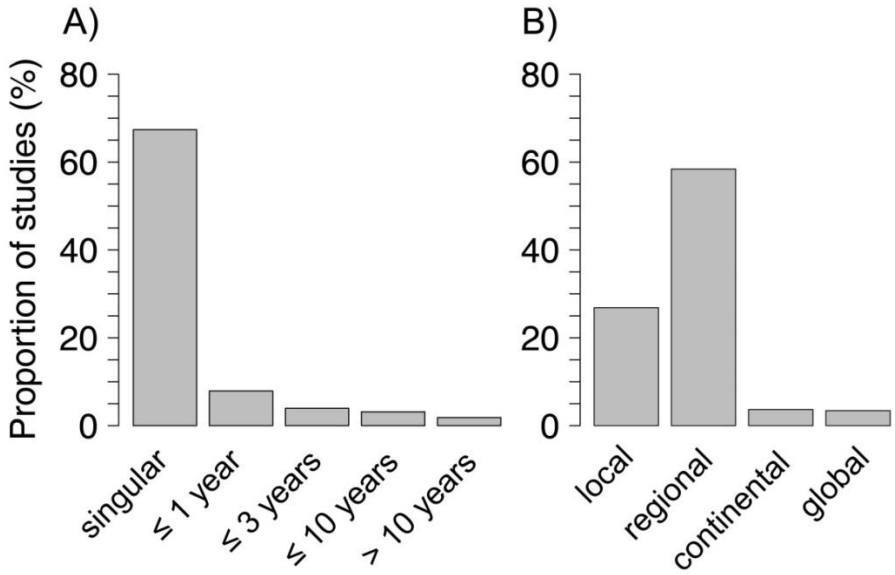

Figure 2: Temporal and spatial scales examined in studies on springs during the last 26 years (1990-2015, n=380 studies); A) Study period (in 60 studies = 15.8% of all studies no information about the study period was extractable from the title or abstract). B) Spatial extent of the studies; 'local' refers to studies conducted on singular sites whereas 'regional' and 'continental' describes studies conducted on landscape and multi-landscape scale, respectively; a 'global' study extent was assumed when the investigations where conducted at least on two different continents (in 29 studies = 7.6% of all studies no information about the spatial extent of the study was given in the title or abstract).

A minor portion of the surveyed studies were explicitly based on a theory-based approach, which was assumed for studies which explicitly state theories in the title or abstract (47 studies equals 12.4% of all cases). This generally low appearance of theoretical considerations in ecological research on spring ecosystems showed no significant, temporal trend over the last 26 years (generalized linear model based on binomial distribution and logit link function, p=0.418). Furthermore, the potential of springs as model ecosystems is realized in just 8.9% of all surveyed studies (34 studies) with no significant trend trough time (glm, binomial distribution with logit link function, p=0.545). One example for the limited amount of studies which use springs to test ecological theories is the work of Glazier et al. (2011). In this study, the authors tested the metabolic scaling theory for amphipods by making use of the thermal constancy which characterizes spring ecosystems.

1.3.2 Springs as model ecosystems

> *"Actually the systems we isolate mentally are not only included as parts of larger ones, but they also overlap, interlock and interact with one another.*
> *The isolation is partly artificial, but it is the only possible way we can proceed"*
> Arthur G. Tansley (1935, p. 300).

Ecologists need to abstract complexity to a certain degree to gain understanding about ecosystem functioning (Tansley 1935, Beierkuhnlein & Nesshoever 2006). On the other hand, high levels of abstraction can lead to unrealistic simplification of complex ecological phenomena which in the worst case can result in wrong conclusions about ecosystem functioning.

Model ecosystems allow disassembling and studying single parts of an ecological system to understand the underlying mechanisms causing whole system functioning (Lawton 1995). Various kinds of model ecosystems with different levels of complexity, thus, abstraction are used by ecologists to understand nature (Kareiva 1989, Lawton 1995). Among these various kinds of model ecosystems complexity but also environmental noise strongly varies. Very simple but highly controllable laboratory experiments have lower complexity than field experiments with artificially composed communities and moderate levels of environmental noise. Highest complexity is given in natural systems characterized by high levels of stochasticity and, thus, environmental noise. A more detailed discussion on the issue of model ecosystems and their characteristics is provided in Box 2.

Due to the inevitable trade-off between complexity and distorting noise, ecologists seek to choose appropriate model ecosystems (with an adequate level of complexity) to sufficiently answer questions of interest and avoiding at the same time over-simplification. Whereas laboratory or field experiments might have a sufficient level of complexity to study intra- or interspecific interactions of species from a community ecological perspective, the same model ecosystems might be insufficient to address more

complex ecosystem functioning. Although natural systems are more adequate for questions related to complex ecosystem functioning, they are characterised by high levels of noise and unexplained variance (see detailed discussion about environmental noise and its consequences for pattern recognition in Chapter 1.8). However, for several natural ecosystems, like e.g. springs, environmental flows are traceable and environmental noise is considerably dampened. Such kind of experiment-like, controllable ecosystems provide models to develop or test ecological theories based on natural systems, like Lindeman's (1942) concept of tropic levels established mainly from the study of lakes. The model characteristics of springs are thereby comprehensively conceptualized by the 'small-catchment approach", an established ecosystem ecological procedure to study ecosystem processes which will be discussed in the following.

The small catchment approach: A systemic perspective on ecosystem functioning

The study of small catchments goes back over 100 years when hydrologists started to develop an interest for these "smallest units of a landscape" (Moldan & Černý 1994). Seminal systems mainly on the biogeochemistry of small catchments were established much later in the early 1960s with the Hubbard Brook experimental site (Bormann & Likens 1967, Moldan & Černý 1994, Likens & Bormann 1995).

According to Moldan & Černý (1994), a small catchment is defined as a small watershed (less than 5 km² surface area) preferably located in a relatively undisturbed landscape. Precipitation, which falls on the area of the catchment, percolates trough the ground of a certain area demarked by the hydrogeological characteristics of the region before the water re-emerges as groundwater at a spring which then enters into a subsequent watercourse. Thus, springs are practically punctual structures, where the discharge from the groundwater flow system of the whole catchment appears at the surface (van der Kamp 1995). These considerations on small catchments apply to the ideal case of areas that do not exhibit considerable losses of groundwater towards deep aquifers of karst water bodies, which is the case in the landscapes studied in this thesis. By having percolated through the upper soil layers, the groundwater strongly interacts with the local soils and weathered parent rock material and, thus, represents the biogeochemical processes of the catchment in the recent past. These biogeochemical characteristics and processes are affected by biological activity including vegetation and by modifying anthropogenic activities (e.g. land use) in the respective landscape units. Furthermore, atmospheric characteristics such as meso-climatic conditions or atmospheric deposition of acidifying or fertilizing substances are found to have significant effects on the biogeochemical catchment properties (Audorff & Beierkuhnlein 1999, Durka 1999). This close link between the physico-chemical characteristics of the groundwater, the related catchment and the surrounding environment provides the opportunity to study ecological systems within the natural boundary of the catchment by accounting at the same time for interactions between biotic system elements (i.e. vegetation) and the abiotic conditions as well as for the influence of the surrounding environment (Moldan & Černý 1994, see Fig. 3). By taking up solutes and adjusting to the temperature regime of the catchment soils, groundwater deriving from a particular catchment (that fulfils the above mentioned requirements) can be seen as a medium carrying information about the flow and status of energy and matter from a whole landscape unit.

In summary, small catchments can be seen as laboratories for quantitative studies on ecosystems, which account for the complexity of natural ecological systems (Moldan & Černý 1994). Therefore the small catchment approach is a well-established approach widely used for the monitoring of biogeochemical processes in national long-term ecological research (LTER) programs, which are discussed in Chapter 1.8 in more detail.

However, monitoring activity of these programs is mainly limited to observations of abiotic conditions in subsequent watercourses (discharge, water temperature, water chemistry). Biotic responses in the subsequent springs or water courses are neglected so far. Furthermore, tests of the complex adaptive systems theory by using the small catchment approach are still missing although the potential of this approach to test major principles of the theory like adaptive behaviour, scale- and path-dependence of ecological systems was already realized by Moldan & Černý (1994). In the following, I will present the potential of helocrenic springs with forested catchments to work on the major principles of complex adaptive systems theory for ecosystems, which were already introduced earlier in the introduction. I will therefore combine the systemic perspective provided by the small catchment approach with an organismic community ecological perspective on the organisation and responses of the plant species inhabiting these semi-aquatic ecosystems. This thesis is restricted to the response of plant species as sufficient information is available for this group of organisms from the long-term monitoring of the studied springs. However, studying the response of animal communities inhabiting these springs would be definitely of similar importance considering the strong specialisation of particular animals (especially aquatic insects and molluscs but also amphibians) to these habitats.

The model character of helocrenic springs

Already Odum (1971) emphasised the experiment-like, quasi-controlled conditions qualifying springs as natural laboratories to test ecological theories. The potential of springs as model ecosystems is owed to various reasons discussed in the following.

First, springs in general but helocrenic springs (as studied here) in particular inhabit an extraordinary high diversity of species (Lindegaard 1995, Lencioni et al. 2011, Gerecke et al. 2011, Cantonati et al. 2012a) and therefore provide ideal tools to study the organisation and structure of biodiversity as one of the major principles of complex adaptive systems.

Second, helocrenic springs as studied here are characterized by a spatially diffuse emergence of slow-flowing water causing a constantly water-saturated, swampy zone (seepage area) with a spatial extent of several to a few hundred square meters (Audorff et al. 2011, **Manuscript 1**). Therefore, these water-dependent ecosystems are clearly separated from the surrounding matrix of terrestrial ecosystems, thus, exhibit an island-like system isolated in the sea of terrestrial ecosystems. This island-like character favours the rigorous test and development of ecological theories as one can see from the example of island biogeography and the related theoretical concepts (MacArthur & Wilson 1967).

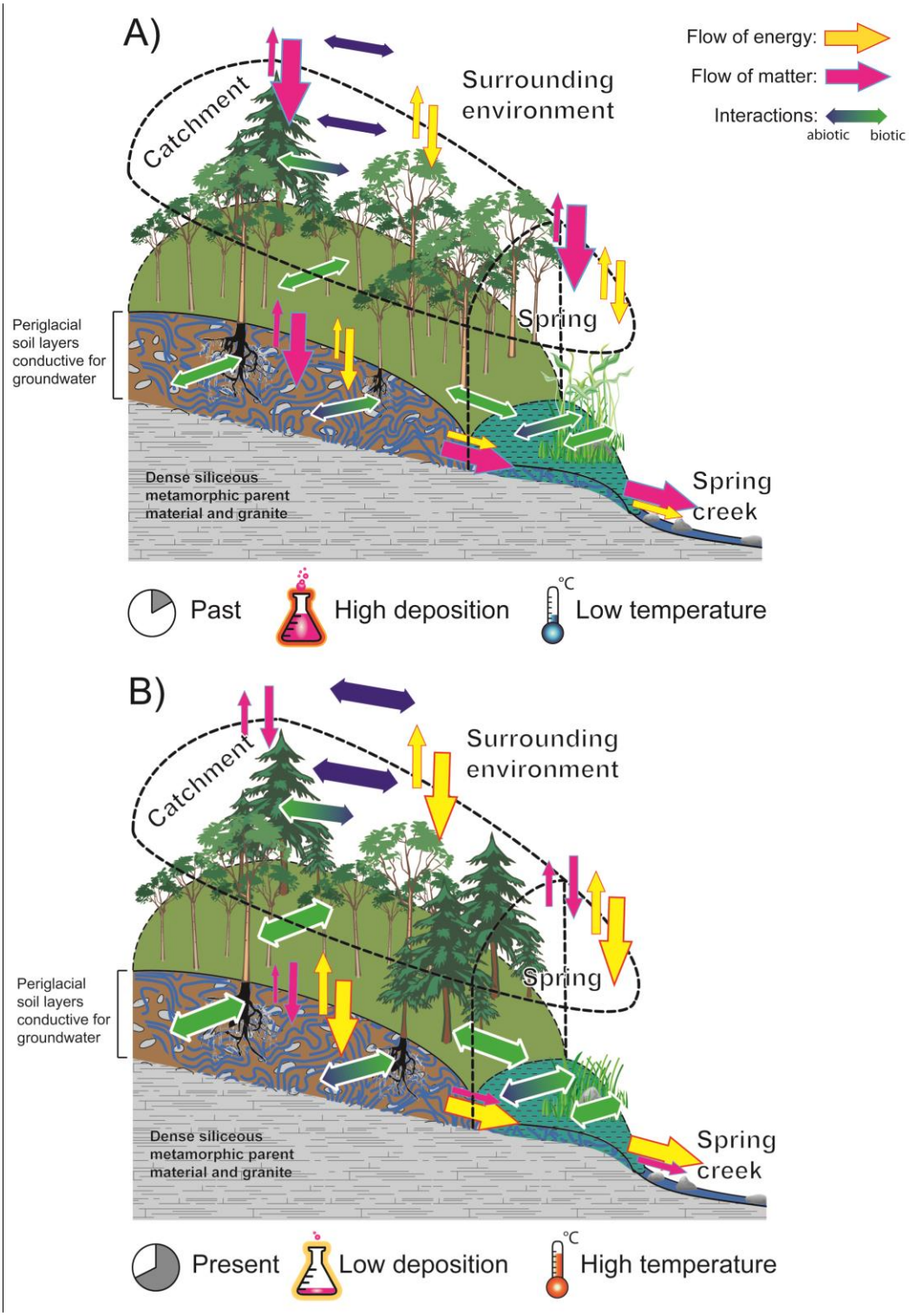

Figure 3: Schematic diagram illustrating helocrenic springs from a systemic perspective. Although the catchment area of the springs provides a natural boundary, flows of energy (i.e. temperature) and matter (i.e. nutrients and acidic depositions) occur across this boundary and changes over time (past: A to present: B). Abiotic changes modify abiotic and biotic interactions and, thus, change the ecological structure and processes of the subsequent springs.

Thirdly, springs in their pristine shape are characterised by rather constant abiotic conditions in terms of temperature, water and nutrient availability and, thus, by low environmental variance and noise (Williams 1991, Beierkuhnlein & Gräsle 1993, Cantonati et al. 2006, Strohbach et al. 2009, Audorff et al. 2011) which numerous stenoecious species with narrow ecological niches are evolutionary adapted to (Odum 1957). Species as biotic elements of spring ecosystems strongly respond to shifts in abiotic environmental settings like acidity, nutrient availability or water temperature (Beierkuhnlein 1994, van der Kamp 1995, Hájek et al. 2002, Hájková & Hájek 2003, Hájková et al. 2004, Cantonati et al. 2006, Hájková et al. 2008, Gerecke et al. 2011, Cantonati et al. 2012b, Glazier 2012, **Manuscript 1-3**).

The helocrenic springs studied in this dissertation are fed by surface-near groundwater, a fact which results from the geological and geomorphological settings of the region which is characterized by crystalline pattern material weathered by solifluction processes during the Pleistocene (Kleber et al. 1998, **Manuscript 1**, Fig. 3). Thus, retention time of precipitated water in the catchment is rather short and responses of the spring inhabiting species to modifications are immediate (Beierkuhnlein & Durka 1993, Strohbach et al. 2009, **Manuscript 1**).

Another beneficial character of springs to test the theory of complex adaptive systems is the tight link of abiotic environmental conditions across a multitude of spatial scales, which is another major principle of this general theory (c.f. scale-dependence, Chapter 1.7.4). Although springs are rather localized systems, the prevailing abiotic conditions of these habitats are strongly controlled by the abiotic conditions of the feeding groundwater, which reflects abiotic conditions acting from regional up to global scale. This is especially true for spring water temperature which is known to approximate the annual mean air temperature on regional scale (Gerecke 2016), which in turn is linked to global climatic conditions. The abiotic drivers of species occurrence acting on local scale are therefore tightly interlinked with the abiotic drivers, which originate from large-scale climatic processes and affect species spatial occurrence on regional and continental scale. This tight cross-scale link of abiotic conditions strengthens the model character of springs to study scale-dependence and cross-scale similarity of system properties.

Furthermore, the helocrenic springs studied in this dissertation have a history of acidification spanning over decades in the 20th century, which is documented by the monitoring of these springs. This monitoring started as early as 1989 (see **Manuscript 2** and **3**, for detailed information about the used methodologies see the Methods section of **Manuscript 1-4**). The emission of acidifying substances (mainly sulphuric and nitrogenous gases), which culminated in Central Europe during the 1970s and 1980s caused large-scale acidification of forest soils, ground- and surface waters (Matzner & Murach, 1995). The detrimental, ecological effects of this large-scale acidification became evident in massive diebacks of forests (‘Waldsterben’) causing a strong legacy of ecosystem studies aiming at a better understanding of these impacts (e.g. Cowling 1982, Schulze & Lange 1990, Gorham 1998). However, the initiated large research projects that studied the impacts and ecological responses represented only small areas that were considered through expert knowledge to be ‘representative’ because the complex system of interacting processes was thought to necessitate single-site research (e.g. in single forest plots in the Fichtelgebirge and in the Solling Mountains, e.g. Schulze et al. 1989, Martinson et al. 2005, Meesenburg et al. 2015). This research was very successful and resulted in legal regulations on the emission of

acidifying pollutants in the late 1980s. As a consequence of the reduced emissions, forest and adjacent freshwater ecosystems started slowly to recover (Hruška et al. 2002, Holmberg et al. 2013, **Manuscript 3**). However, single-site studies could not answer questions on large spatial scales e.g. for landscapes or continents. Also it was not possible to continue this labour- and money-intensive research over long time periods. In consequence, there is no knowledge in precise trajectories of recovery after the deposition of pollutants had been considerably reduced.

In the spring catchments of this study, nevertheless, monitoring data of this recovery process are now available for a period of almost 3 decades. This dissertation benefits from this opportunity to elaborate the path-dependence of ecosystems, a major principle of complex adaptive systems discussed in Chapter 1.7.5. The high spatial abundance of the studied springs in the forested landscapes of Central Germany provides furthermore a replicated setting of natural model ecosystems on landscape scale. All these facts provide an experiment-like, 'controlled' setting which enables to study general ecological theories like the theory of complex adaptive systems.

Box 2

Excursus 1: Potentials and challenges related to model ecosystems between full control and full complexity

Ecologists test theoretically based assumptions to understand the functioning of ecological systems and further develop on the underlying theories (Kampichler et al. 2001, Beierkuhnlein & Nesshoever 2003, further detail see Box 3). However, natural ecosystems, which are the basic objects of interest, are characterized by high complexity, means a high amounts of confounding effects (noise) which might blur the focal patterns and, thus, impede sufficient testing of ecological theories (for more details see Chapter 1.8). Experimental ecosystems with artificial communities (either under laboratory or field conditions) and controlled abiotic conditions help to decrease these confounding effects and, thus, facilitate the test for the focal patterns or processes (Diamond 1983, Huston 1997, Beierkuhnlein & Nesshoever 2006). Furthermore, tests can be more easily replicated and parameters of interest manipulated (Lawton 1995).

However, increasing artificial control decreases complexity, the basic characteristic of natural ecosystems, which makes controlled experimental ecosystems likely to be unrealistic (Diamond 1983, Beierkuhnlein & Nesshoever 2006). Artificial experimental ecosystems used e.g. in the Ecotron facility (Lawton 1995) are often restricted to small spatial and short temporal scales and have a much simpler structure than natural systems (Kampichler et al. 2001, Englund & Cooper 2003). Furthermore, artificial experimental ecosystems can just account for a limited set of potential influencing variables due to the immense amount of work and costs linked to multifactorial experiments (Huston 1997). Thus, variables which might be of importance in the mimicked, natural systems might be completely neglected in the artificial imitations (Beierkuhnlein & Nesshoever 2006).

Box 2 continued

Another problem related to artificial communities set up in a semi-natural environment (e.g. field experiments with planted communities, controlled soil and precipitation regime) is the incomplete control of confounding effects. Under such semi-natural conditions just a (unknown) part of the system can be controlled whereas other influential variables remain uncontrolled, which leads to so called "hidden treatments" (c.f. Huston 1997). Furthermore, model ecosystems made up by artificial communities bear the risk of biased species collections leading to a biased distribution in species characteristics (traits) which in turn might artificially affect community structure and response to the manipulated environmental factors ("sampling effect" or "selection probability effect" c.f. Wardle 1999, see also Norberg 2004 and references therein). The restricted exchange of energy and matter between the artificial system under focus and the environment (c.f. Kampichler et al. 2001) as well as the missing consideration of historical effects on community composition and responses (c.f. Tilman 1989) are two additional problems related to most artificial experimental ecosystems which are characterized by rather short life expectancies.

All these problems mentioned for artificial experimental ecosystems seem to be avoidable when studying natural ecosystems. Studies on natural ecosystems like on Barro Colorado Island (Leigh Jr 1999) allow for considering the full extent of system complexity related to the exchange of energy and matter (Chapter 1.7.2), abiotic and biotic cross-scale interactions (Chapter 1.7.4) as well as the path-dependence of ecological structures and processes (Chapter 1.7.5). Furthermore, ecologists who study natural ecosystems can profit from the anthropogenic changes on natural ecosystem functioning which provide man-made experimental manipulations on large spatial scale (Margalef 1975).

However, natural ecosystems are typically characterized by high amounts of environmental noise, which usually cannot be controlled in these complex systems (see Chapter 1.8). Due to this high degree of complexity, cause and effects are typically hard to control or manipulate in natural ecosystems, which complicates sound hypothesis testing (Diamond 1983, Beierkuhnlein & Nesshoever 2006).

Missing of controls and appropriate replication are additional problems having the potential to diminish the reliability of statistical detection of natural ecosystem patterns and processes (Blackburn & Gaston 1998, **Manuscript 6**). Furthermore, idiosyncratic histories of different ecosystems make it even harder to infer generality from natural complexity (Beierkuhnlein & Nesshoever 2006). The apparent lack of ecological long-term data in combination with the high amount of environmental noise therefore hinders our general understanding of natural ecosystem functioning.

Both, artificial experimental and natural ecosystems have to be considered as tools for ecologists, which are good to answer one question but might be inappropriate to answer another one (Lawton 1995). Thus, depending on the questions under focus, one has to think about the appropriate level of abstraction and, in turn, complexity of the chosen model ecosystem needed to sufficiently answer the focal question. Here I argue that springs as natural ecosystems characterized by low environmental noise provide ideal models to work on a general ecological framework like the complex adaptive systems theory. As these model ecosystems combine the positive features of artificial experiments (controllable) and natural ecosystems (full complexity), the long-term monitoring of springs provides a unique opportunity to study natural ecosystem functioning under experiment-like settings (see previous Chapter 1.3.2).

1.4 The role of theory in ecology (then and now)

> *"In science, theory demarcates what we know from what we do not; it is the clearest description of the limits of our understanding"* James P. Collins (2011, p. ix).

Theoretical considerations are as old as humans' interest in natural phenomena. Already in the 4th century BC Greek philosophers like Theophrastus developed a theoretical picture of an autonomous nature characterised by the interaction of plants, animals and the abiotic environment (Ramalay 1940). Theory as a major driver in the development of science promotes scientific progress (Marquet et al. 2014). However, progress often happens in an unsystematic manner (Kuhn 1962, Kolasa 2011).

Additionally, systems (biological as well as social) are described especially in their initial phases to evolve in a rather chaotic way, meaning especially young systems are 'tinkering' during their evolution without defined direction or general 'goal' (c.f. Kuhn 1962, Allen and Starr 1982, Kauffmann 1996). This seems to be true for modern ecology as well which is described in its early years as "chaotic, polymorphic to anarchic" with numerous theories emerging in the 'Golden Age' of theoretical ecology in the 1920s to 1930s (McIntosh 1987). After this initial explosion of ecological theories and a second peak in the 1960s to 1970s, the emergence of ecological theories slowed down in recent years (Kolasa 2011). Until the beginning of the 20th century, ecology has evolved into an established scientific discipline, where theory and empirical research are closely intertwined to unravel the causes of observed ecological patterns (Beierkuhnlein & Nesshoever 2006, Collins 2011).

The description of ecological patterns has a long-standing history in ecology (Rosenzweig 1995, Lomolino 2001, West & Brown 2005). During the last years, massive amounts of ecological data, which were gathered during decades of observation on large spatial scale, are synthesized in big ecological databases (Enquist et al. 2009, Kattge et al. 2011, Chytrý et al. 2015). Concomitant with the increasing data availability in combination with rapid development of new statistical algorithms and access to enormous computational power recently emerged sub-disciplines such as macroecology strongly focus on the description of general ecological patterns (Beck et al. 2012). With this increasing capacity and handling efficiency of enormous amounts of data, the question arises whether we really need an improved general theoretical framework like the theory of complex adaptive systems in a 'big data' world where everything seems to be comprehensible from pure empirical (observational) research (for a more detailed discussion see Box 3).

Box 3

Excursus 2: Do we need ecological theory in the modern science world?

Massive scientific efforts like the mapping of entire genomes by next-generation sequencing, the establishment of ecological long-term monitoring and experimental networks as well as the merging of ecological data in big ecological databases are of major importance for the progress of modern day ecology (Marquet et al. 2014). Based on these big amounts of information put together during the last years paired with our modern day computational skills, there are voices claiming that pure empirical research is sufficient for scientific progress (Anderson 2008). To say it in Jeff Lichtmann's words, Jeremy Knowles Professor of Molecular and Cellular Biology at Harvard University: "In biology, I think we're entering the age of big data, which will replace big ideas with what's actually the case" (Powell 2015).

One problem related to big ecological data sets obtained from different sources is heterogeneity. For large-scale studies, data from various local-scale studies are summarized. However, this local-scale data was most of the time not collected to answer the big-scale question but to pursue a specific question related to the particular, local-scale study, which is often restricted not only spatially but also on temporal scale. Thus, spatial and temporal resolution and extent, accuracy of data collection and study design are often very heterogeneous among the studies summarized to answer big-scale questions, which often diminishes the significance of the large-scale studies using this heterogeneous data (c.f. Rahbek 2005, Beck et al. 2012). This problem is aggravated as meta-data about the original datasets are often missing or are not accounted for in ecological studies based on big data. One possible solution might be large-scale or long-term, coordinated experimental or monitoring networks with standardised protocols for data collection (c.f. de Boeck et al. 2015). An example might be the long-term dataset this dissertation is based on.

A second problem is the increasing loss of species knowledge and, thus, ecological understanding which makes it hard to detect biases in research based on big ecological datasets. Ecology started "as the last nature preserve for lovers of butterflies and birds" (McIntosh 1987, p. 335). Nowadays, species knowledge is successively decreasing and people with profound knowledge about species and their ecological requirements are aging and have to be counted as endangered species (Frobel & Schlumprecht 2014). This problem might be also favoured by the fact, that early career ecologists are under the pressure of the 'publish or perish' philosophy of modern world science (Laurance et al. 2013) to secure future funding. This leaves little time for the labour-intensive determination of species or for working through the ecological concepts and theories which made up our modern world ecology (c.f. McIntosh 1987). However, this lacking knowledge about species identity and ecology and related theoretical concepts combined with an overwhelming amount of data one have to tackle with might be a problematic combination diminishing the progress of modern ecological research. In other words, we might lose touch with the ecological systems we are actually interested in. In the worst case, this could lead to the description and discussion of observable patterns, which are actually based on artificial biases rather than ecological causes (see Chapter 1.8 and 2.2).

A general ecological theory like the complex adaptive systems theory might not solve the problems related to data heterogeneity and increasing lacks of species knowledge. Although theory is just a simplification which will never describe reality, it is a necessary scientific tool to identify appropriate questions and to judge the progress made to answer these questions by using a specific approach (Beierkuhnlein & Nesshoever 2006, Kolasa 2011).

Box 3 continued

However, theoretical concepts need rigorous testing to increase progress of ecological understanding (Simberloff 1981, Caswell 1988, Tilman 1989, Kolasa 2011). Theory provides a framework when searching for general rules which then have to be tested empirically (Beierkuhnlein & Nesshoever 2006). In other words, "data without theory is description, and theory without data is storytelling" (Houlahan et al. 2015, p. 342). Thus, general understanding of ecosystem functioning requires both, the observation of ecological patterns and processes and theoretical concepts about the underlying mechanisms which than can be tested (McIntosh 1987, Tilman 1989, Picket et al. 2007, Marquet et al. 2014).

Empirical research based on big datasets has therefore to be coupled to efficient theory to guide ecological science and, thus, to increase ecological understanding which is a prerequisite for efficient management strategies in our currently fast changing world (Beck et al. 2012, Marquet et al. 2014). To sum it up: "big data without a big theory to go with it loses much of its potency and usefulness" (West 2013). Or to say it in Leonardo da Vinci's words: "He who loves practice without theory is like the sailor who boards ship without a rudder and compass and never knows where he may cast".

1.5 The different theoretical perspectives in ecology

> *"Pluralitas non est ponenda sine necessitate" (Plurality is not to be posited without necessity)* Petri Lombardi cited in Thorburn (1918).

In Ecology like in other disciplines of natural science different theoretical perspectives exist. Reductionism and holism are two fundamentally different theoretical perspectives between which scientific disciplines typically cycle (West & Brown 2005). The divergence in ecology into theoretical perspectives towards simplification, like reductionism, and generalizing perspectives, like holism, originates from the complexity and spatio-temporal heterogeneity characterizing ecological objects (Beierkuhnlein & Nesshoever 2006). A controversial discussion is still going on, whether ecology should be based on reductionist or holistic approaches (see current discussions in Marquet et al. 2014 and Houlahan et al. 2015).

Reductionism, which states systems and their functioning to be explainable as the sum of the single system elements and their properties, was promoted among ecologists during the early days of modern ecology (McIntosh 1987) and is still seen as the 'scientific ideal' in ecology (Abel 1998). Holism, on the other hand describes systems as entities that cannot be properly explained by the properties of their single elements, thus, representing a 'science of the integration of parts' (Voigt 2015). In contrast to the narrowly disciplinary, reductionist approach, the interdisciplinary and integrative holistic approach is today less common in ecology but is nevertheless represented in sub-disciplines such as evolutionary biology and systems theoretical approaches to work on population or ecosystem dynamics (Abel 1998, Kolasa 2011).

Concomitant with the simplifying perspectives of reductionism and the generalizing perspectives of holism, there is still disagreement whether ecological theory can be descriptive or has to be based on pure mathematical formalizations (see again Marquet et al. 2014 and Houlahan et al. 2015). The initial theoretical considerations in biology and ecology were purely descriptive like the theory of evolution by means of natural selection provided by Darwin and Wallace (Caswell 1988, Marquet et al. 2014) and were just a posteriori conceptualized in mathematical formulizations like Fisher's fundamental theorem (Fisher 1958) and Wright's adaptive landscapes (Wright 1932).

Mathematics help to reduce ambiguity in prediction and communication. Thereby theories conceptualised in mathematical functions are easier to test and, thus, were more actively discussed in the scientific community compared to more descriptive theories (Heidegger 1977, Kolasa 2011, Marquet et al. 2014). This may have led to exorbitant use of mathematical formulisations in ecological theory during the 1970s to 1980s (c.f. MacArthur 1972, McIntosh 1987, Wissel 1998). In biogeography, one reason for this push of mathematical concepts was the tremendous success of the theory of island biogeography of MacArthur & Wilson (1967) which became also one of the most successful concepts of all times in ecology.

Although the simplification induced by these kinds of theories may have intensified scientific discussion, oversimplification caused by the overuse of mathematical theories does obviously not adequately represent the complexity of ecological systems (McIntosh 1987, Kolasa 2011). When looking at individual processes within ecosystems, even simple ecological feedback loops cannot be sufficiently mathematically formalised, which questions the potential of purely quantitative concepts to improve the understanding of complex ecological systems (Margalef 1975).

Due to increasing computational power and statistical algorithms, modern day ecology is no longer restricted by simple mathematical formulisations. Phenomena related to complex ecological systems can therefore be tackled within a more general, theoretical framework, which would be just insufficiently described by pure mathematical descriptions (Levin 2002, Keil 2014). However, the more general a theory the harder it is to test and the higher is the need to break it down into smaller pieces to handle it empirically in practice. In the following section I will illustrate the facets of the theory of complex adaptive systems. After the introduction of the general framework of this holistic theory and discussing it in the already introduced context of ecological theory, I will discuss the five major principles of this theory related to ecological systems, which were already introduced in former sections of the introduction and are empirically tested in this dissertation for springs as model ecosystems.

1.6 Complex adaptive systems theory as holistic perspective

"The whole is more than the sum of its parts" Aristotle

Ecological systems, ranging from single cells to the global biosphere are characterised by the interaction of individual system elements (e.g. compartments of single cells, individuals in a population, species of a community) leading to the emergence of system structures (e.g. trophic structures like food webs) and the flux of energy, matter and information on multiple scales which in turn might affect subsequent interactions among the system elements (Huston 1997, Levin 1998, Voigt 2015, see also Fig. 3). These abiotic and biotic, non-linear dynamics and interactions operating across different spatial and temporal scales and being modified by historical events characterize ecosystems to be complex adaptive systems (Gell-Mann 1994, Levin 1998, Peterson et al. 1998, Norberg 2004, Peters et al. 2007, Nash et al. 2014).

Therefore, complex adaptive systems theory as a derivative of systems theory is an analytical approach which represents the dynamic interactions and feedback loops between system elements and the environment (Hartvigsen et al. 1998, Holland 2006). An holistic perspective on ecosystems is needed to work with this approach as the traditional, reductionist perspective, means a perspective where the sum of the single element behaviour will explain whole system functioning, is not working for the complex adaptive systems approach (Holland 2006).

Whereas classical community ecology as well as systems ecology largely ignored their respective perspectives until the 1990s, community ecologists as well as systems ecologist are nowadays increasingly realising the need to integrate community ecological aspects (e.g. population dynamics and community composition) and system related ecological aspects (e.g. physical transport processes) to understand ecosystem functioning (Roughgarden 2009). This integrative and comprehensive idea of ecosystem functioning was already reflected in the ideas of Lotka (1925) and later taken up in system ecology (Odum 1983) and in hierarchy theory (Allen & Starr 1982). Until the end of the 20th century, the perspective shifted from linear and continuous processes and structures as main characteristics of ecosystems towards an increasing dominance of non-linear and discontinuous processes and structures as the main attributes of ecosystems (Sole´ & Bascompte 2006). All these classical system approaches in ecology considered self-organisation, interaction, feedback and non-linearity as important properties (principles) of ecosystems but ignored the process of adaptation, which is a major principle in complex adaptive systems theory (Hartvigsen et al. 1998).

As the name suggests, complex adaptive systems are characterized by complexity and adaptation. The latin *complexus* derives from the Greek *pleko* which means plait or twine, literally describing the interwoven elements characterizing complex systems (Lenton & Oijen 2002). Thus, complex systems can be defined as systems which cannot be sufficiently described by the properties of its individual components (Gallagher & Appenzeller 1999). Adaptation as the second characteristic of complex adaptive

systems, describes the 'evolving structure' of systems, where interactions and feedbacks among and between system elements and the environment induce adaptive processes affecting future interaction and feedbacks (Gell-Mann 1994, Holland 1992, Holland 2006, see also Box 1).

Complex adaptive ecosystems lack central control mechanisms but are controlled by many interacting biotic elements underlying their own 'rules' which are constantly adapted by the interaction with all other elements and the abiotic environment (Holland 1992, Gell-Mann 1994, Holling 2001, Gunderson & Holling 2002, Holland 2006). Thus diversity, individuality and organisation of components (elements), interaction between system elements and the environment as well as between system elements across scales, non-linearity and stability in reaction, and path-dependence (history) play major roles for complex adaptive systems functioning (Margalef 1975, Gell-Mann 1994, Holland 1995, Levin 1998). These characteristics of ecological systems also appear in the recently introduced concept of macro-system ecology (Heffernan et al. 2014), which can be seen as an application of the complex adaptive systems theory to study ecosystems in a global context.

By identifying common patterns in the organisation and the dynamics of systems, complex adaptive systems theory comprises biotic phenomena spanning from the emergence of life from prebiotic chemical reactions, evolution and bodily functions of single organisms to the functioning of ecological communities and global biomes (Gell-Mann 1994, Levin 2002, Filotas et al. 2014). The theory of complex adaptive systems has a sound mathematical foundation in the scientific disciplines of thermodynamics (Prigogin 1945) and chaos theory (Bak 1996, Kauffmann 1996), which I will not elaborate as this dissertation focuses on the empirical applicability of this general theory. However, more detailed information about the mathematical formulisations related to the complex adaptive theory in ecology can be found e.g. in Levin (2002).

The goal of ecological theories is not to deliver a detailed description of ecological systems but to disentangle fundamental mechanisms of ecosystem functioning (Brown 1997). The complexity inherent in all ecological systems inhibits a complete understanding of these systems (Margalef 1975). However, we do not need to understand every single detail because knowledge about general properties (major principles) relevant for system functioning is sufficient (Margalef 1975, Kauffmann 1996, Levin 2002). The focus of this thesis is to empirically test the general theory of complex adaptive systems for springs as model ecosystems. To break the general theory down into testable parts, I will focus on five major principles which have been stressed by several authors to be relevant for the understanding of complex ecosystem functioning (Margalef 1975, Gell-Mann 1994, Brown 1997, Levin 1998, Levin 2002, Filotas et al. 2014): 1) Diversity and organisation of biotic system elements; 2) Flow, distribution and interaction of information, energy and matter (abiotic drivers); 3) Stability and non-linearity of system reaction; 4) Scale-dependence and cross-scale similarity of important system properties and 5) Path-dependence of the system properties.

1.7 The major principles of complex adaptive systems theory in ecology

In the following I discuss the theory of complex adaptive systems by referring to the five major principles listed in Table 1 and mentioned earlier. When pursuing the aim of a general understanding of ecosystem functioning, the already existing theories in ecology need to be brought into a common framework of a more general theory (Scheiner & Willig 2011). Here I argue that the theory of complex adaptive systems is such a general theory. Several existing, already well-established theories in ecology can be framed in the below listed major principles of the complex adaptive systems theory which then allows testing this general theory for natural model ecosystems such as springs. Each of the five major principles and the related, consecutive theories listed in Table 1 is related to at least one manuscript in this dissertation and will be discussed in the following.

Table 1: Five important major principles of the complex adaptive systems theory in ecology, the related ecological patterns and theoretical conceptualisations and the related manuscripts in this dissertation testing these principles for springs as model ecosystems.

Major principle	Observable pattern / process	Related theoretical conceptualisation	Related manuscript in this dissertation
Diversity and organisation of biotic system elements	Rank - abundance relationships	Niche apportionment models like e.g. broken-stick model by MacArthur (1957)	Manuscript 1, 4
	Abundance - distribution relationships	Carrying capacity hypothesis (Nee et al. 1991)	
		Niche requirement hypothesis (McNaughton & Wolf 1970, Brown 1984, Pitman et al. 2001)	
	Spatial and temporal patterns in ecological response characteristics (e.g. species community composition, species co-occurrence)	Concept of ecosystem engineers (Jones et al. 1994, 1997)	

Table 1 continued

Flow, distribution and interaction of information, energy and matter	Spatial and temporal patterns in ecological response characteristics (e.g. species community composition, species co-occurrence)	Hutchisonian niche theory (Hutchinson 1957)	Manuscript 1, 2, 3, 5
Stability and non-linearity	Stability and non-linearity in ecological response characteristics (e.g. temporal changes in species community composition)	Concept of ecological resilience and elasticity (Holling 1973) Concept of alternative stable states and hysteresis (Beisner et al. 2003)	Manuscript 2
Scale-dependence	Scale-dependence and cross-scale similarity of ecological response characteristics (e.g. spatial patterns of species distribution, species realised niche)	Concept of scale and cross-scale interactions (Wiens 1989, Rosenzweig 1995) Concept of scaling of environmental noise (Williamson 1987, Storch et al. 2002) Eltonian noise hypothesis (Soberón & Nakamura 2009)	Manuscript 5
Path-dependence	Path-dependence of ecological response characteristics (e.g. species community composition and stability)	Concept of path-dependence (Holland 1992, Gell-Mann 1994) and ecological memory (Padisak 1992, Ogle et al. 2015)	Manuscript 2, 3, 4

1.7.1 Diversity and organisation of biotic system elements

Understanding the relationship between observable structures and ecological functioning is of major importance in ecological research (Levin 1998). In ecology much effort is put into the understanding of broad-scale patterns related to diversity (Levin 2002). The organisation and spatio-temporal variation of ecological communities and ecosystems has been a central topic in community ecology and biogeography for decades (Brown 1984, Condit et al. 2002, Legendre et al. 2005, Siefert et al. 2012). Furthermore, the organisation and heterogeneous distribution of organisms and the underlying ecological drivers are fundamental aspects that need to be explained by a general theory in ecology like the complex adaptive systems theory (Norberg 2004, Scheiner & Willig 2011).

Not all species are equally abundant

Uneven abundance distributions in species communities result from species sorting by environmental conditions and species interactions (c.f. assembly rules, Goetzenberger et al. 2012 for review). In turn, changes in community composition resulting from changing environmental conditions strongly depend on the initial community structure in terms of species abundance and cover (Grime et al. 2000, Potts et al. 2006). As a net result of these abiotic - biotic interactions, changes in the community composition occur, increasing the abundance of these species which are best adapted to the prevailing conditions (Norberg 2004). High local abundance is here defined as a large number of individuals of a given species at a particular site (Gaston et al. 1997). This general pattern of community composition with a few abundant but many rare species is well conceptualised and theoretically founded like in MacArthur's (1957) broken stick model (Kolasa 2011).

A positive correlation between local abundance and spatial distribution of species has been reported by numerous studies (Brown 1984 and references therein, Gaston et al. 1997, Gregory and Gaston 2000, Arellano et al. 2015, **Manuscript 1**) and is seen as the most general, scale independent pattern in ecology (Gaston et al. 2000). Most species are both, locally rare and regionally restricted whereas just a few, so called 'oligarchic' species are likely to show high local dominance and wide regional distribution (Pitman et al. 2001). The occurrence of oligarchic species seems to especially favoured by stable environmental conditions (Pitman et al. 2013) and is reported from tropical forests (e.g. Arellano et al. 2013 and 2015) and springs (**Manuscript 1**).

Carrying capacity and differences in species' niche breadth are proposed as mechanisms explaining the observable, positive abundance - distribution relationship. The carrying capacity hypothesis (Nee et al. 1991) argues that locally abundant species have a lower probability of extinction and/or a higher probability of colonising other suitable habitats, causing the positive abundance - distribution relationship. As an alternative hypothesis, it is argued that species with broader ecological niches should be able to use a broader range of resources, which is then reflected in high local abundance and wide distribution

(McNaughton & Wolf 1970, Brown 1984, Pitman et al. 2001). Both hypotheses, which have a strong organismal / community ecological focus, seem to be not in congruence with the observations we made for spring ecosystems. Springs are island-like, waterlogged ecosystems characterised by stable environmental conditions and isolated from each other in a terrestrial landscape matrix. Thus, extinction and dispersal as major explanatories of the carrying capacity hypothesis are negligible in these ecosystems at least for plants as relatively sessile organisms. Furthermore, a positive correlation between niche breadth and commonness (integrating local abundance and regional distribution) was not confirmed for the studied springs (for more details see **Manuscript 1**). In other words, the most common species were not the most generalistic ones. This raises the question for additional mechanisms explaining the organisation of biotic system elements (i.e. species). A more systemic approach might be useful besides the proposed, organismal approaches to pursue this question.

One possible, additional mechanism explaining community organisation can be related to the path-dependence of ecosystems. Different intensities of historic environmental stressors (i.e. acidification) are shown to have long-lasting effects on community organisation and the occurrence of oligarchic species (**Manuscript 1**). These abiotically induced changes in community organisation can affect community resilience in face of recent, environmental perturbations (extensive summer droughts, **Manuscript 2**). The historic context under which a certain community developed in combination with the adaptive behaviour of the single compartments of the community (i.e. species) might therefore not only influence current but also future community organisation. Resilience as a response property of biotic compartments (i.e. communities) to the abiotic drivers is discussed in Chapter 1.7.3 whereas the path-dependence of ecological systems is addressed in detail in Chapter 1.7.5. Feedback loops between abiotic environmental conditions and ecosystem engineering species resulting in successive changes in the abiotic conditions as well as species interactions might be an additional mechanism affecting community organisation (**Manuscript 4**).

Not all species are equally important for system functioning

Positive feedback loops (adaptive cycles) between system entities are of major importance in organising complex adaptive systems (Bonabeau 1998, Holling 2001). Adaptive cycles result from ongoing feedbacks between biota and the abiotic environments, in which biotic elements (e.g. species) modify the abiotic environment, which in turn have influence on the establishment and development of the biotic elements. In a more narrow sense, species favoured by specific, initial environmental conditions change the environmental conditions by growing and, thus, change the environmental setting for other, co-occurring or successive species. These adaptive cycles are a major part of theories about the emergence of life on earth (Gaja hypothesis; Lovelock 1972) and are nowadays an accepted theoretical concept related to complex adaptive systems theory (Abel 1998, Levin 1998, Holling 2001, Lenton & Oijen 2002, Gunderson & Holling 2002).

In ecological systems, the strength of feedback loops between abiotic environmental conditions and biotic system elements (e.g. species) is strongly determined by the properties (traits) of these elements

(Norberg 2004). One example for an effective species trait is the ability of peat mosses (genus *Sphagnum*) to actively acidify soil and water, which not only changes the abiotic conditions but also the species composition in their habitat and, thus, the respective community structure (Klinger 1991, Hamilton 1996, **Manuscript 4**). Ecosystem engineers (sensu Jones et al. 1994, 1997) like *Sphagnum* mosses, meaning species that can actively modify environmental conditions and, thus, resource availability for other species, are assumed to influence system dynamics and trajectories in almost every ecosystem on earth (Jones et al. 1997). Ecosystem engineering species, which are initially favoured under certain environmental conditions, can further modify habitat conditions, with favourable or unfavourable consequences for the other co-occurring species (von Gillhausen et al. 2014). Positive feedbacks between abiotic conditions and ecological engineers affecting community composition are reported for freshwater ecosystems (eutrophic, shallow lakes; Scheffer 1989), marine ecosystems (coral reefs; Fung et al. 2011) and waterlogged, terrestrial systems (van Breemen 1995, Granath et al. 2010, **Manuscript 4**). Furthermore, shifts in the structure of ecological systems to alternative states, which were induced by abiotic (anthropogenic) perturbations (e.g. by nitrification: Liebowitz et al. 2014, and by acidification: **Manuscript 1 and 2**) can be stabilised in these alternative states for decades. Mechanisms which stabilise ecosystems in alternative states can be system's inertia or positive feedback loops between the abiotic environment and ecosystem engineers, which were favoured by the initial environmental perturbation (Hagerthey et al. 2008, **Manuscript 4**). Ecological communities that were shifted from one state into another alternative state differ in their response to following environmental perturbations compared to unaltered communities (Walter et al. 2013, **Manuscript 2**, Chapter 1.7.5).

1.7.2 Flow, distribution and interaction of information, energy and matter

"Panta rhei" (Everthing flows) Plato

Ecosystems are characterised by flows of information, energy and matter between the system elements and the environment, which are regulated by biotic processes (see conceptual Figure 3 for springs). These flows as well as the storage and transformation of information, energy and matter in ecological systems results in stable structures like e.g. food webs where energy passes from primary producers trough a complex network of different trophic levels before it is released again by the activity of decomposers (Levin 1998). However, trophic interactions are just one type of processes structuring ecological systems. Dominance relations among co-existing plant species resulting in particular plant community structures and the emergence of characteristics species are strongly shaped by abiotic environmental conditions (Ellenberg & Leuschner 2010, **Manuscript 1**). For example, temperature and acidity regime are reported as major abiotic determinants of the plant community composition of springs (Audorff et al. 2011, Spitale

et al. 2012, **Manuscript 1**). While growing, species consume abiotic resources or actively transform unsuitable into more suitable environmental conditions and, thus, modify the distribution of energy and matter and species in a given ecosystem (Brown 1995, Schweiger et al. 2015, **Manuscript 4**). These interactions between co-occurring species and positive feedbacks between species and the abiotic environment have significant, lasting effects on the structure of plant communities (see previous Chapter 1.7.1).

The structuring effects of the abiotic environment and biotic interactions on species occurrence are framed in the realised ecological niche concept of Hutchinson (see Box 1). In this theoretical concept, the realised niche of a species is defined as a set of abiotic conditions and biotic interactions which span up a multidimensional niche space in which a particular species is able to survive and reproduce (Hutchinson 1957). Besides above mentioned positive correlation between species local abundance and spatial distribution, the ecological niche is referred to be one of the most important and fundamental concepts in ecology (Chase & Myers 2011). Furthermore, the theoretical assumptions of the classic niche concept of Hutchinson are well-represented in the theoretical assumptions of the complex adaptive systems theory, which makes both concepts compatible. Complex adaptive systems such as species have certain environmental requirements or restrictions in terms of resources and environmental conditions that are represented in the different dimensions of the multidimensional niche space. These conditions have to be fulfilled to maintain system functioning, which means in the case of species populations: survival, growth, and reproduction (Brown 1995).

Direct and indirect joint effects of abiotic environmental drivers

The multidimensional character of the classical niche concept of Hutchinson as well as of the complex adaptive systems theory applied on ecosystems suggests not only interactions among biotic system elements (e.g. species) but also interactive effects of abiotic environmental conditions on the performance of single species, whole communities or even higher ecological entities (e.g. biomes). Abiotic environmental factors influence biotic ecosystem elements just barely isolated from other abiotic factors but most of the time in multiple interactions with different environmental factors (see Paoletti et al. 2010, de Vries et al. 2014 for forests).

Joint effects of multiple environmental stressors on ecosystems are increasingly recognized to be of major importance (Heij & Schneider 1991, Bouwman et al. 2006, Paoletti et al. 2010). Such kind of joint effects are likely to be stronger than just the sum of the effects of each singular stressor due to complex synergistic interactions between a multitude of different environmental stressors acting on different spatial and temporal scales (see Staal et al. 2015 for tropical forests). Here I propose to distinguish between direct and indirect joint effects of abiotic environmental factors on the performance and structure of biotic system elements like single species or whole communities.

Under the term direct joint effect of abiotic factors I summarize the joint effects of different environmental factors which directly influence species performance or community structure. An example

for these kind of abiotic interactions is the joint effect of historic acidification and a climatic extreme event, which is reported in **Manuscript 2** to influence the multidimensional, environmental spaces occupied by single species of plants inhabiting springs as well as the structure and stability of spring plant communities. In this manuscript we show that various plant community groups which were affected in different intensities by historic, atmospheric acidification exhibit specific responses to the climatically extreme summer of 2003, where an extensive drought combined with a heatwave occurred over large part of Central Europe (Schaer et al. 2004).

The term indirect joint effect of abiotic factors defines the situation when one abiotic environmental factor modifies another abiotic environmental factor which then influences the performance or organisation of biotic system elements (e.g. species community composition). In other words, an environmental factor A indirectly affects biotic system elements by modifying another abiotic environmental factor B which then directly influences the biotic elements. Although indirect joint effects of abiotic environmental factors might be hard to disentangle in many cases from direct joint effects, several examples exist for this indirect form of joint effects. One example is the interaction of climate warming and historic, atmospheric acidification which is reported by Schindler et al. (1996) and Schindler (1997) to decrease the concentration of dissolved organic carbon and, thus, increase the transmittance of freshwater bodies for UV radiation with detrimental effects on the inhabiting freshwater species. Another example is drought induced re-acidification events, which are reported to significantly impede the recovery of macroinvertebrate communities of Canadian freshwater streams (Bowman et al. 2006). A third example is the effect of continuous road salt application on the biogeochemical processes of forested catchments presented in **Manuscript 3**. By changing the biogeochemical catchment characteristics related to acidification and nutrients leaching, road salt application was shown in this study to indirectly influence the plant community structure of subsequent spring ecosystems over decades.

Based on the apparent, interactive effects of abiotic environmental conditions on ecosystem functioning we have to shift our perspectives from singular acting environmental stressors towards a more holistic view on the interactive effects of multiple environmental stressors acting on different temporal and spatial scales. Furthermore, these joint effects of multiple abiotic factors as well as the biotic responses to these multiple factors are rarely linear but characterised by strong non-linearity. First results from long-term monitoring studies give hints for non-linear interactions of multiple stressors (Malcolm et al. 2014). However, most studies on the ecological effects of environmental changes treat each stressor as a singular factor but neglect potential joint effects and non-linear behaviour of multiple stressor interactions and biotic responses (c.f. Bytnerowicz et al. 2007).

1.7.3 Stability and non-linearity

Response of ecological systems to external perturbations can have many different facets ranging from strong inertia over gradual changes to abrupt shifts from one state (e.g. species population structure, community composition) to another (Kéfi et al. 2015). The way of how a certain ecological system reacts to perturbation strongly depends on the present and past environmental circumstances as well as on the intensity of internal interactions between the system elements (e.g. species). This multitude of interacting, internal and external factors can result in non-linear response behaviour which is an inherent trait in many ecological systems (Hartvigsen et al. 1998, Dodds et al. 2010, Mysterud et al. 2001).

With respect to the increasing anthropogenic pressure on ecological systems during the last decades and the uncertainty according to their responses, a better understanding of ecological response dynamics is more topical than ever. Sudden shifts in ecosystems can strongly affect ecosystem functioning and, thus, services provisioning with drastic economic consequences (Peters et al. 2004, Capon et al 2015, Kéfi et al. 2015, Nimmo et al. 2015). The development and adaptation of management strategies in nature conservation or land use requires thinking in systems and not in particular components. This is what is provided by the concept of complex adaptive systems theory. Even though this approach does not offer simple solutions that are often preferred in practice, it enables to capture and conceptualise the apparent chaotic response behaviour which often characterises ecological systems (Hartvigsen et al. 1998). During the last decades, the complex systems perspective gave impetus to both, theoretical conceptualisations and practical strategies to handle ecological response dynamics triggered by environmental perturbations (Filotas et al. 2014).

Theoretical conceptualisations of system dynamics related to complex adaptive systems theory were already established in the 1970s (Holling 1973) and are nowadays accepted in ecology and nature conservation (Beisner et al. 2003, Quinlan et al. 2015). In these theoretical concepts, ecological systems are considered as temporally dynamic systems shifting between alternative stable states characterised by different sets of possible conditions (e.g. species assemblages, c.f. Beisner et al. 2003). The strength and duration of system responses to a certain environmental perturbation is thereby conceptualised by the idea of ecological resilience and elasticity (cf. Holling 1973). Differences in the response trajectories between impact and recovery response following an external perturbation are described by the concept of hysteresis (c.f. Beisner et al. 2003). All these key aspects of the response behaviour of ecological systems will be briefly discussed in the following.

Alternative stable states

The concept of alternative stables states was originally introduced in ecology in the early 1970s (e.g. Holling 1973, Margalef 1975). It was derived from general cybernetic theory applied in engineering and other system sciences. Today this view is well established in ecosystem management and conservation (Capon et al. 2015, Kéfi et al. 2015).

This concept of ecosystems which can be existent in several alternative stable states is often visualised by a simple ball-and-cup model, where a ball in a two- or three-dimensional landscape represents the ecological system in its current state (c.f. Gunderson 2000). The current state of an ecological system can be defined by a set of state variables, i.e. configurations of the system such as species composition of a plant community or species abundance structure in this community. An ecological system is in a stable state, when these state variables remain stable over time (Beisner et al. 2003). In the ball-in-cup model, this is represented by a local minimum of the landscape in which the ball stabilises.

Perturbations in the external conditions like e.g. climatic extreme events can shift a system from its current stable state into an alternative state (e.g. different community composition), which then can be stabilised (Capon et al. 2015). Translated to the ball-in-cup model, the ball can be pushed out of one local minimum and can stabilise in another one. Whether such a shift occurs depends on the system's stability which is framed by the theoretical concepts of ecological resilience and elasticity. In other words, the system may return to the initial stable state, i.e. the initial set of configurations (e.g. initial community composition) after a small disturbance which can be compensated by the system. However, the system might shift to another configuration and, thus, an alternative state, when the perturbation is large enough to overcome the system's stability (Beisner et al. 2003). Thus, complex interactions between the abiotic environment and biotic system elements, which are modified by the history of the system, contribute to the current state and modify future responses of an ecological system. This path-dependence in ecological response dynamics is shown in **Manuscript 2**, where different levels of impairment by anthropogenic acidification caused different stable states in plant community composition of springs, which differently responded to a climatic extreme event.

The inherent complexity of ecological systems can result in a certain degree of stochasticity and non-deterministic response behaviour. Based on this stochasticity, the response of most ecological systems to external perturbations in not deterministic but ecological systems can develop into several alternative states under the same external conditions (Bonabeau 1998, Kreyling et al. 2011, Staal et al. 2015). A famous example for several alternative stable states an ecological system can adopt is represented by shallow lakes, which can either stabilise in a clear water state dominated by macrophytes or in a turbid state dominated by phytoplankton after changes in external environmental conditions i.e. nutrients load occur (Scheffer et al. 1993, Scheffer 1998).

Stability

Understanding ecosystem stability, which describes the ability of a certain system to maintain self-similarity after external perturbations, is of fundamental importance when studying ecosystem dynamics (Margalef 1975). The extent of system stability, i.e. the degree to which a system can maintain its current state, determines whether an ecological system withstands an external perturbation and stays in its current state or shifts into another alternative stable state after passing a certain tipping point of high instability (Beisner et al. 2003, Scheffer et al. 2009, Staal et al. 2015).

The temporal response, thus, stability of an ecological system against external perturbations can be framed in the concepts of ecological resilience and elasticity (cf. Holling 1973). Elasticity therefore quantifies the ability of a perturbed ecosystem to return to its initial state after disturbance (Grimm & Wissel 1997). Ecological resilience defines the extent of external perturbation which can be absorbed by a system without changing its actual state (Holling 1973, Gunderson 2000). Both concepts are actively discussed and used in modern day nature conversation and management (Nimmo et al. 2015, Quinlan et al. 2015).

The concepts of elasticity and ecological resilience are key aspects of complex adaptive systems theory as they capture 1) the capability of systems to absorb disturbances, 2) the capacity to learn and adapt to changes in external conditions and 3) the capability of self-organisation (Quinlan et al. 2015). Furthermore, elasticity as well as ecological resilience can depend on the individual history of ecological systems, thus system's path-dependence and ecological memory effects. These are also principles of complex adaptive systems theory (Bonabeau 1998, **Manuscript 2**, see Chapter 1.7.5 for more details). Also the adaptive behaviour of species in combination with positive or negative feedbacks between species and the environment may significantly influence the elasticity and resilience of ecosystems (Walker et al. 2004) which can maintain alternative stable states after a system shift occurred (Standish et al. 2014, Kéfi et al. 2015, Staal et al. 2015, **Manuscript 4**).

Non-linearity

Responses of ecological systems to external perturbations are assumed to be not only linear but often characterised by non-linearity (Whittaker 1975, Austin 1976, Meents et al. 1983). The concept of non-linearity follows the idea that ecological systems can show a quite abrupt response to external perturbation which is not expected from the past system's behaviour (Dodds et al. 2010). In a more mathematical sense, ecosystem response cannot be described by linear relationships (0^{th} or 1^{st} order polynomials) but show a non-linear e.g. exponential or hyperbolic response behaviour. Famous examples for non-linear ecological responses are species-area curves (Drakare et al. 2005), the relationship between habitat loss and species extinction risk (Reynolds 2003) or the biotic response to increasing temperature captured by the Arrhenius equation.

Non-linearity is hard to asses in natural systems and even harder to predict due to the fact of superposition in ecological system reaction paired with the inability to quantify all relevant stimuli of the systems response (Patten 1983). However, land use and nature conservation management have to be aware that any kind of anthropogenic intervention can cause rapid shifts of ecological systems into undesirable alternative stable states and recovery of shifted systems back into the initial state can be strongly diminished or even impossible (Dodds et al. 2010). System hysteresis, which quantifies the discrepancy of the system's response trajectories between the impact and recovery response, can thereby hinder or even prohibit the recovery of anthropogenically perturbed ecosystems (Suding et al. 2004).

1.7.4 Scale-dependence

> *"The only things that can be universal, in a sense, are scaling things"*
> Mitchell Feigenbaum cited in Gleick (1987, p. 186)

Ecological patterns as we observe them result from processes (see Box 1), acting and interacting across a wide range of spatial, temporal and organisational scales. Scale is hereby defined as a unit of space, time or organismic association in terms of grain size (resolution) and extent (c.f. Allen & Starr 1982, Turner 2001, Box 1). This interplay among ecological patterns and processes is also conceptualised in the complex adaptive systems theory (Hartvigsen et al. 1998, Levin 2002).

The complex adaptive character of ecosystems causes a tight interlink between patterns and processes on different scales, where interaction and adaptation acting on smaller scales has influence on the emergence and, thus, the observability of patterns on larger scales (Levin 1998). The concept of scale has therefore become a central topic in ecology (Schneider 2001, Kallimanis et al. 2008) and the question of cross-scale interactions, asking for the effect of changes at one level of organisation on patterns and processes at another level of organisation is increasingly considered (Wiens 1989, Hartvigsen et al. 1998, Gunderson & Holling 2002, Loreau et al. 2003). Consequently, the scale-dependence of ecological processes and patterns has become an important central topic in ecological research during the last decades (Margalef 1975, Hartvigsen et al. 1998, Levin 2002, Sandel 2015).

Cross-scale interactions are proposed as major stabilising forces of ecological systems and, thus, have to be considered as important insurance mechanisms to maintain ecosystem functioning in a constantly changing world (Holling 1992, Peterson et al. 1998, Levin 1998, Gunderson & Holling 2002, Peters et al. 2007, Nash et al. 2014). Cross-scale interactions can increase the productivity of ecosystems and foster the resilience and elasticity of ecological systems to external perturbations related to global environmental change (Rietkerk & van de Koppel 2008, Schoelynck et al. 2012). This happens due to localized consumer-resource interactions and disturbance-recovery processes, where single system elements (e.g. organisms) accumulate resources in the local environment as a consequence of increasing abiotic stress (e.g. aridity) and therefore are able to persist. As a consequence of the localised persistence of single elements of the system, overall stability of the whole ecological system can increase (Rietkerk & van de Koppel 2008 and references therein).

Understanding ecological patterns and processes is strongly intertwined with the understanding of scale-dependence (Beck et al. 2012). When aiming to separate cross-scale interactions and scale-dependence in complex adaptive systems like ecosystems, mechanisms have to be identified that are influential for ecosystem functioning irrespective of scale (Wiens 1989, Levin 1992, Levin 1998, Whittaker et al. 2001, Cross-scale Manuscript). Such kind of scale invariant processes can help to answer the question of when and at which extent ecological patterns and processes are scale-dependent. By integrating seemingly distinct phenomena across a wide range of scales, these scale invariant processes

might therefore strongly help to increase our understanding about ecosystem structures and processes and their relativity across scales (c.f. Sandel 2015). In **Manuscript 5** we argue that the realised temperature niche of species could be such kind of scale invariant generality.

What causes scale-dependence of ecological patterns and processes?

There is an ongoing debate about the degree of scale-dependence of ecological patterns and processes. Environmental drivers and their effect on ecological patterns and processes are reported to vary with scale in different intensities (Calfoun & Martin 2007, Belmaker & Jetz 2011, Siefert et al. 2012, Takagi & Miyashita 2014, Belmaker et al. 2015, Hicks et al. 2015, Taylor et al. 2015). Numerous reports of scale-dependence in ecological systems make the search for generalities, that would explain patterns and processes independent of scale (like Newton's or Einstein's principles in physics), to a specific challenge in ecology (c.f. McGill 2010, Sandel 2015). However, asking what drives the scale-dependence in ecological systems is an important issue in biogeography and other sub-disciplines of ecology (Sandel 2015).

Based on the observations we made for springs I argue that the strength of observed scale-dependence is related to three factors: A) the mismatch between the observed and the relevant scale, B) the strength of cross-scale interactions of environmental drivers and C) the scale-dependence of environmental noise.

A) The degree of mismatch between the observed and the relevant scale

Whether an ecological pattern can be detected or not depends on the scale of observation (Gaston 2000, Beierkuhnlein 2007). Patterns which emerge on one scale (grain size and extent, see Box 1) can disappear at another scale (Hutchinson 1953, Levin 1992, Kallimanis et al. 2008, Alhamad et al. 2011, **Manuscript 5**). Scale-dependent effects on the perception of ecological patterns were reported e.g. by Rahbek (2005). In this connection, the perceptional ability of ecologists is strongly biased towards phenomena acting on anthropocentric scales that correspond with our everyday experience (Wiens 1989). As individual experience and, thus, perception is an idiosyncratic feature, there is a considerable disagreement among ecologists from different sub-disciplines about the role of scale-dependence in ecological systems (Rahbek 2005).

Furthermore, ecological patterns observed at on scale might result from mechanisms operating at another, unobserved scale, a fact which results from the complex character of ecosystems with numerous feedbacks between different hierarchical levels (Levin 1992, Gaston 2000). This missmatch between observed and relevant scale, i.e. the scale which is ecologically relevant for pattern formation, limits our understanding of the mechanisms leading to the observed pattern. Depending on the degree of missmatch between observed and relevant scale, this might, in the worst case, lead to misconclusions about underlying ecological processes. Or to say it in the words of Wiens (1989, p. 390): "Because we are clever

at devising explanations of what we see, we may think we understand the system when we have not even observed it correctly." Thus, choosing an inappropriate scale of observation can lead to the misinterpretation of patterns as ecological meaningful (Wiens 1989, see also Chapter 2.2).

To overcome the above mentioned problems related to the mismatch between observed and relevant scale, Potter et al. (2013) state that identifying the systematic structure of changes in environmental variation across scales will be the most promising solution. Regarding that, I argue that cross-scale links of environmental drivers and the scale-dependence of environmental noise are two important issues to consider.

B) The degree of cross-scale links of environmental drivers

The individual importance of environmental factors in driving ecological patterns is assumed to vary with scale (Wiens 1989, Levin 1999). Processes driving small-scale patterns are commonly assumed to act fast whereas processes driving large-scale ecological patterns are expected to act over longer time periods (Brooks et al. 1988) although large-scale environmental impacts occuring fast can also have strong ecological consequences over short temporal scales (e.g. Chixuclub asteroid impact and its ecological consequences at the Cretaceous–Paleogene boundary). Thus, continental-scale, biogeographic patterns are suggested to be mainly driven by abiotic factors acting on large spatial and long temporal scales (e.g. climate, plate tectonics etc.), whereas patterns that emerge on the scale of local communities could be mainly driven by relatively short-term biological processes related to species-specific traits like e.g. dispersal and competitive abilities (Cracraft 1994, Belmaker & Jetz 2011, Siefert et al. 2012).

Furthermore, climatic conditions experienced by organisms on micro-scale can be very heterogeneous and strongly diverge from the surrounding marcoclimatic condictions, which makes it difficult to predict species responses to climatic changes when just macroclimatic information is available (Potter et al. 2013). However, large-scale abiotic factors driving large-scale ecological patterns are physically interlinked with small-scale abiotic factors shaping community-scale patterns (Wiens 1989), like microclimatic conditions are linked at least to some degree to regional and global climate. Based on the observations we made for spring ecosystems, I argue that the strength of cross-scale links among abiotic environmental drivers affects the cross-scale similarity in ecological patterns or processes. Strong cross-scale links between abiotic conditions (i.e. strong links between the regional and local temperature regime) might therefore result in enhanced cross-scale similarity of the ecological patterns or processes across these scales. In contrast weak cross-scale interactions between abiotic conditions could therefore result in strong scale-dependence of ecological patterns and processes. By comparing the realised temperature niches of plant species of springs across seven orders of magnitude of spatial scale (from sub-metres to several thousands of kilometres), we observed high cross-scale similarity for this ecological trait (**Manuscript 5**). At the same time, the temperature regime of springs is strongly controlled by the temperature of the feeding groundwater, which in turn reflects the average temperature of the catchment area (Gerecke 2016). This strong cross-scale link between local groundwater temperature influencing local species occurrence (**Manuscript 1**) and the annual mean temperature driving species occurrence on

continental scale (Simova et al. 2011) seems to cause the strong cross-scale similarity in species temperature niches observed in **Manuscript 5**.

Such high cross-scale similarity observed for species realised temperature niches in spring ecosystems can be caused by the openness of these systems, i.e. high transfer rates of energy and matter from adjacent systems, in this case the forested catchments from which the groundwater derives (see Fig. 3). High transfer rates that characterise open systems tend to increase cross-scale links of external drivers (Wiens 1989). This results in high cross-scale similarity of ecological response traits like species realised niches. Thus, the strength of cross-scale links of environmental drivers, which is driven in our case by the degree of system openness, might be one important determinant whether cross-scale similarity or scale-dependence of ecological patterns is found.

C) Scale-dependence of environmental noise

The scale-dependence of environmental noise is another essential aspect according to the detection of scale-dependence of ecological patterns and processes. Whereas the effect of climate on ecological patterns like vegetation formation is evident at large spatial scales, biological processes like competition or dispersal limitations are assumed to override the effects of the abiotic environment on small spatial or temporal scales (Wiens 1989, Storch et al. 2002). This idea is conceptualised in the Eltonian noise hypothesis (Soberón & Nakamura 2009), which predicts that biological processes driving ecological patterns like species distribution on small spatial scale are averaged out at large scales, where species distribution is then explained by abiotic conditions (**Manuscript 5**).

As biological processes are often the result of complex interactions among idiosyncratically acting species, small-scale ecological patterns which are driven by biotic processes can be decoupled from direct physical determination. The decoupling of biotic processes from the abiotic environment increases uncertainty when statistically explaining these biotic processes by using abiotic environmental predictors (c.f. Wiens 1989). This uncertainty induced by the complex adaptive behaviour of biotic system elements (e.g. species) is further amplified by high spatial and temporal heterogeneity in abiotic environmental conditions, which in consequence can blur the underlying ecological patterns and processes under focus (Clark 1985, Chase & Myers 2011, see also Chapter 1.8).

I argue that uncertainty which is related to the explanation of biological processes based on abiotic environmental factors and which increases with decreasing spatial scale (higher resolution, c.f. Potter et al. 2013), can therefore lead to the apparently detected strong scale-dependence of ecological patterns and processes observed in many studies. For springs, which are characterized by high abiotic (thermal) constancy at local scale, we observed high degrees of cross-scale similarity for species realised temperature niches (see **Manuscript 5**). Based on these observations I hypothesize that high scale-dependence of ecological patterns and processes results to a considerable extent from high levels of environmental noise characterising ecological systems at small spatial and temporal scale.

1.7.5 Path-dependence

"Nothing in biology makes any sense except in the light of evolution"
Theodosius Dobzhansky (1973)

Ecosystems alike species change trough time by the transformational process of evolution (Lewontin 1978, Levin 1998). Ecological structures and processes emerge from an ongoing, adaptive interaction of the system's elements with each other and the constantly changing environment (Filotas et al. 2014). Based on these complex interactions, ecosystems have to be referred to as historically grown systems, where the ecosystem's memory in combination with the current context influences the system's future trajectories (Margalef 1975, Anand et al. 2010, Parrott & Lange 2013). This idiosyncrasy of ecosystem evolution, where the present state of a system can evolve into several possible future states, diminishes predictions about detailed structure and functioning of ecological systems in the future but calls for a general understanding of ecosystem evolution and functioning (Margalef 1975, Pickett et al. 2007, Merchant 2016). Thus, history and context play an important role in complex adaptive systems like ecosystems (Holland 1992, Gell-Mann 1994), which have to be assumed to be "moving targets" (Abel 1998). The importance of path- and context-dependence for spring ecosystems is discussed in **Manuscript 2**, where historical environmental stressors like atmospheric acidification has been shown to affect ecosystems' response to following, external perturbations (i.e. extreme drought and heat) even two decades after the historic perturbation.

The adaptive behaviour of ecosystems as a consequence of changing external influences leads to modifications of ecosystem structure and functioning (Parrott & Lange 2013, Filotas et al. 2014). Thus, the concept of path-dependence is intertwined with the concepts of alternative stable states, stability and regime shifts as discussed in Chapter 1.7.3 (Levin 1998). The adaptive behaviour of ecosystems that can be driven by ecological memory (c.f. Padisak 1992) can influence ecosystem stability (Parrott & Lange 2013). Thereby, ecological memory enhances (Filotas et al. 2014) or diminishes (**Manuscript 2**) ecosystem stability to external perturbations like e.g. climatic extreme events. Whether ecological memory increases or diminishes ecosystem stability to external perturbations strongly depends on the amount and frequency of perturbation the particular systems have adapted to (Hawkes & Keitt 2015). Furthermore, positive feedbacks between biotic system elements (i.e. ecosystem engineering species) and historic environmental stressors can sustain alternative stable states in community composition over decades (**Manuscript 4**) which modifies ecosystem responses to following environmental changes (**Manuscript 2**). Thus, the ecological legacy of historic environmental stressors as a component of the path-dependence of ecosystems can have long-lasting, detrimental effects on ecosystem functioning and services provisioning although the initial environmental stressor is already out of public and scientific focus. Based on the complex adaptive behaviour of ecosystems leading to deviations between predicted and observed changes in system functioning, path-dependence (ecosystem history) is an important major principle of ecosystems that has to be accounted for in future projections of global change effects (Hawkes & Keitt 2015, **Manuscript 4**).

1.8 Methodological requirements for testing the complex adaptive systems theory in ecology: The role of long-term monitoring and sampling design

> *"The natural world is dynamic, not static, and the older each of us gets, the more apparent is this truth"* John J. Magnuson (1990, p. 500).

The study of complex ecological systems which are characterised by high heterogeneity strongly relies on proper methodologies to gather data which then are analysed to infer patterns and causation (Stephens et al. 2007). Based on our limits of perception, fast changes in ecological structures and processes acting on the temporal and spatial scales we experience in our everyday lives are thereby easily recognisable compared to slow or even delayed changes acting on a large spatial and long temporal scale. When processes are effective on whole continents and over decades to centuries, then we perceive the world to be rather static than dynamic (Magnuson 1990). However, numerous changes acting on these large spatial and long temporal scales strongly affect ecosystem functioning. Current-day examples are gradual climate warming, atmospheric acidification, continued deforestation or the ongoing invasion processes of plant and animal species.

The investigation period of most ecological studies, hardily exceeding more than three years is too short to properly address these relevant questions, particularly regarding the reaction of complex ecological systems to external stressors (Tilman 1989, Gitzen et al. 2012). Long-term monitoring, i.e. the periodic recording of ecological features and / or abiotic conditions over long periods of time (c.f. Hellawell 1991, see also Box 1) can help to document ecological changes acting over extensive periods of time (Magnuson 1990). Furthermore, long-term monitoring enables to account for the path-dependence of ecosystems and to study cross-scale interactions between ecological processes acting on short temporal scales and those acting over long periods of time (c.f. Magnuson 1990, Swanson & Sparks 1990). This is of major importance as path-dependence and cross-scale interactions, both major principles of complex adaptive systems, strongly control current and future ecosystem functioning on which our wellbeing relies.

Several ecological long-term projects have a systemic perspective on ecosystem functioning like the Hubbard Brook experimental forest in New Hampshire (Likens & Bormann 1995), the Cedar Creek Ecosystem Science Reserve in Minnesota (Tilman & Downing 1994) and the monitoring project of Central European forest springs which is the bases for my dissertation. The Long-Term Ecological Research (LTER) consortium as another renowned, systemic monitoring initiative had a strong link to the complex adaptive systems perspective from the very beginning (c.f. Magnuson 1990, Swanson & Sparks 1990).

Although long-term monitoring has the potential to strengthen our theoretical, ecological understanding (Capon et al. 2015), many monitoring programmes suffer from unclear research goals and survey design (Magurran et al. 2010). Good monitoring programmes should be based on secured long-

term funding, adequate spatial and temporal replication, detailed documentation of sampling sites (permanent plot marking) and procedures and careful data collection (Legg & Nagy 2006). Several long-term monitoring programmes fulfil these requirements including the Long Term Ecological Research (LTER) Network with 36 years of monitoring activity (LTER 2015), the international Long Term Ecological Research (iLTER) network (Gosz 1996) which has been active for 23 years, the Global Observation Research Initiative in Alpine Environments (GLORIA, Pauli et al. 2015) that conduct monitoring for 18 years and the National Ecological Observatory Network (NEON, Keller et al. 2008) which is currently in its construction phase. However, many monitoring projects rely on temporally restricted funding and therefore have to change their research objectives and priorities quite often to meet the agenda of funding agencies which also change through time (Gitzen et al. 2012). Changing research objectives often go along with changing sampling methodology, intensity and interval which in turn diminish the statistical power (see Box 1) of the gathered data and, thus, the significance of results obtained from monitoring projects (c.f. Field et al. 2007).

The power of a statistical test, which is strongly intertwined with the type II error of a statistical test (beta: the chance of not detecting a pattern although it is there; statistical power: 1- beta) is restricted by i) high noise (variability) in the tested data, ii) low effect size of the tested variable and iii) small numbers of independent samples used in the test (Osenberg et al. 1994). Thus, increasing the sample size is the simplest way to increase statistical power (Foster 2001, Jennions & Møller 2003). However, total sample size is most of the time restricted by limitations in budget, time and labour (Foster 2001, Legg & Nagy 2006, **Manuscript 6**) which makes an increase in total sample size not feasible in most cases.

Power analyses are frequently used to infer the required effort in terms of sample size to achieve appropriate power and, thus, statistically detect ecological patterns which are masked by a given amount of noise (Foster 2001, Jennions & Møller 2003). However, power analyses underlie the same statistical restrictions (homogeneity of variance as well as normal distribution and random sampling of data) as the tests they assess and require detailed a priori knowledge about the expected amount of noise and effect size (Johnson 1999). Furthermore, the classical approaches of power analyses have been shown to be restricted from a methodological perspective (for more details see Hoenig & Heisey 2001). In **Manuscript 6** we used artificial data with known properties (amount of noise, underlying patterns) to assess the question of how many samples and replicates are needed to maximize prediction success and minimize erroneous detecting of non-existent patterns.

The detection of ecological patterns strongly relies on the statistical tools used to analyse the sampled data like correlation or regression analyses. However, ecological patterns can be hidden or artificial patterns with no ecological significance can emerge if too many factors are measured. The common practice to test numerous, apparently irrelevant variables to explain the ecological response of interest can obscure ecologically relevant processes or causing multicollinearity among the tested variables, which can bias the statistical analyses and threatens their interpretation (Graham 2003, Nakagawa 2004). Decisive processes can also be impossible to be detected when they happened in the past or on spatial scales which are not covered by the sampled data because the resolution of temporal or spatial sampling is too coarse. This misappropriation of variation can bias the estimates obtained from

regression analysis, which is a well explored statistical issue in other scientific disciplines but is rarely recognized in ecology ('regression dilution', e.g. McInerny & Purves 2011). In these cases, existing patterns are undetectable by statistical approaches or statistics might detect artefacts that are ecologically irrelevant.

Both problems related to statistical tests, the failed detection of present patterns and the erroneous detection of non-existent patterns are strongly related to total sample size and the amount of noise in the data that differs considerably between data sets and systems, respectively. Increasing sample size decreases the type II error in statistical tests, means the change of statistically missing an ecological pattern (Foster 2001, Legg & Nagy 2006). However, the chance of erroneously detecting a non-existent pattern (type I error) also strongly increases with increasing sampling size (Foster 2001). As p-values are mathematically dependent on sample size, large sample sizes will automatically result in very small p-values although the tested effect is almost zero (Johnson 1999). This paves the way for spurious correlations, i.e. the statistical detection of non-existent patterns.

Such kind of spurious correlations are especially problematic in modern ecological research where massive amounts of data are statistically tested which might lead to misinterpretation when not accounting for the actual effect size. The strong dependence of standard statistical measures like p-values on sample size gives these commonly used evaluation criteria a very schizophrenic character. Whereas a missing statistical detection of an expected ecological patterns is often attributed to insufficient small sample sizes, the statistical detection of patterns, which were not expected based on prior knowledge and, thus, appears to be surprising, is often assumed to be the result of the underlying large sample size. By omitting the use of standard statistical measures, the simulations presented in **Manuscript 6** provide a sound, reproducible basis for the assessment of these problems.

Besides the mentioned methodological problems related to varying samples size, the high variability and strong noise, which is characteristic for ecological data, further challenges statistics and, thus, the methodical basis for the generation of scientific understanding. In ecological systems, physical properties (e.g. air temperature) are generally assumed to be less variable than biotic properties (e.g. species richness). Biotic properties are related to rather complex processes such as population dynamics or biotic interactions and, thus, are characterised by high heterogeneity and variance in the resulting patterns and effects (Osenberg et al. 1994). Furthermore, abiotic factors are often characterised by non-directional (white) noise which blurs underlying, ecological patterns in a stochastic, unpredictable way. In contrast, heterogeneity in biotic factors results from the complex adaptive behaviour of ecological elements (e.g. species) and, thus, affects underlying patterns often in a directional, systematic way. By accounting for both types of error (random and systematic) in different intensities, **Manuscript 6** shows, that even intermediate amounts of systematic error (i.e. 5% of total variation) strongly increase the risk of erroneous pattern description (type I error inflation). Besides technical approaches to deal with these apparently methodological problems (e.g. adapted sampling design, alternative statistical methods), scientists should generally put more emphasis on general principles based on theory (Hoenig & Heisey 2001). In this dissertation I argue that the theory of complex adaptive systems might be a theoretical framework to

increase our general understanding in ecology without being misdirected by the interpretation of spurious patterns.

2 Synthesis

2.1 The manuscripts of this thesis

In the following I will shortly summarise the most important findings of each manuscript included in this thesis. Each of the included manuscripts tests at least one major principle of complex adaptive systems theory by using springs as natural model ecosystems. By discussing the major findings of each manuscript within the theoretical framework of the complex adaptive systems theory I want to provide a general picture on ecosystem functioning for these model ecosystems which then can be transferred to other ecosystems. The presentations I gave at national and international scientific conferences on topics related to my thesis are listed in Table 2. Additional publications and conference contributions which I wrote and presented during the period of my PhD but which are not directly related to this thesis are listed in Appendix 1 and 2.

Manuscript 1 targets the diversity and organisation of plant communities inhabiting the investigated springs. To study this major principle of complex adaptive systems theory we examined species composition and dominance structure for vascular plants and bryophytes as well as water characteristics of 238 springs in lower mountain ranges of Central Germany. By quantifying species' commonness as a parameter integrating local abundance and spatial frequency of occurrence, we detected three hyper-dominant (oligarchic) species (*Chrysosplenium oppositifolium*, *Sphagnum fallax* and *Calamagrostis villosa*). These species showed much higher local abundance (and, thus, commonness) than all other species with similar spatial frequencies of occurrence. All three species characterise distinct plant community groups of springs that were differently affected by historic acidification during the 20th century and that differently reacted to the climatic extreme summer of 2003 (see **Manuscript 2**). In general, the plant community composition of the investigated springs was strongly modified by changes in the water temperature and acidity regime of the outpouring groundwater. These physico-chemical characteristics are tightly linked to biogeochemical and climatic properties of entire catchments. The abiotic properties of forested catchments as smallest units of a landscape (Moldan & Černý 1994) are strongly influenced by atmospheric (chemical as well as thermic) conditions acting across large spatial scales (see Fig. 3). Thus, trans-boundary flows of energy and matter as well as cross-scale interactions of abiotic drivers, two major principles of complex adaptive systems, play a crucial role in the organisation of the investigated spring plant communities. Furthermore, species with narrow ecological niches, which are restricted to certain environmental conditions and, thus, are known to be spatially restricted in most ecosystems (Pitman et al. 2013) turned out to be regionally widespread among the investigated spring ecosystems. Thus, low environmental variation characterising springs on regional scale seems to allow specialised species to reach not only high local abundance but also a wide regional distribution. The low environmental variation characterising the investigated springs might therefore be responsible for the high commonness of specialised species in these semi-aquatic ecosystems which contradicts the common belief of species organisation (c.f. McNaughton & Wolf 1970, Brown 1984, Pitman et al. 2001, Pitman et al. 2013).

Manuscript 2 deals with the path-dependence and stability of ecological response characteristics, another two of the five principles of complex adaptive systems theory in ecology, which are rarely worked out for natural ecosystems. By using the prolonged drought and heatwave of the summer of 2003 as a natural, 'experimental treatment' imposed on springs which were affected to different degrees by historic acidification, we were able to show a strong effect of ecosystems' legacy on subsequent community responses, thus, path-dependence of ecological processes. We therefore compared ecological resilience and elasticity of single plant species and species assemblages of whole communities related to the climatically extreme summer of 2003 for 57 springs with different degrees of acidification. Springs that were previously less affected by acidification (characterised by *Chrysosplenium oppositifolium*) showed higher resilience and elasticity than strongly acidified springs, which were characterised by peat moss species of the genus *Sphagnum*. Thus, ecological resilience and elasticity of plant communities against the severe drought and heat wave of 2003 significantly differed among the springs dependent on their previous impairment by acidification. These strong negative synergies between emerging climatic extreme events and past environmental stressors like acidification, which have been shown in this study to cause multiple alternative states of community composition in spring ecosystems, confirm the relevance of path-dependence when studying ecosystem functioning.

Manuscript 3 further elaborates on the interactive effect of different environmental stressors on the plant community structure and, thus, the functioning of spring ecosystems. In this manuscript we demonstrate a strong interactive effect between historic acidification and its ecological legacies and the continuous application of road salt as a commonly used de-icing agent in winter. We therefore studied the temporal development of plant community composition and water chemistry of 52 springs over a period of 25 years (1989-2013). Continuous road salt application turned out to enhance the leaching of important soil nutrients like potassium, magnesium and calcium from road adjacent, forested catchments. Furthermore, road salt application had not only significant seasonal but also long-lasting effects on the acidity regime of springs with road-adjacent catchments, which significantly altered the long-term trajectories in spring plant community structure. With this study, we were the first to report such kind of acidifying effect of road salt for inland forested catchments. Similar acidifying effects are well known for coastal forests (c.f. 'sea salt effect' Wiklander 1975, see also: Hindar et al. 1995, Skjelkvåle et al. 2007, Laudon 2008). The significant, long-lasting geochemical and subsequent ecological consequences of this 'road salt effect' on forested catchments and the subsequent springs, which were shown in this study to act over more than two decades, further emphasize the important role of abiotic, environmental interactions and path-dependence (ecosystem history) when aiming for a general understanding of ecosystem functioning.

Manuscript 4 shows that alternative states in the pant community composition of springs, which were initially caused by historical environmental impairments (i.e. atmospheric acidification) can be further stabilised by positive feedback loops between the prevalent environmental settings and ecosystem engineering species (sensu Jones et al. 1994, 1997). Peat moss species of the genus *Sphagnum,* which characterise acidified springs (**Manuscript 1**) and were shown to increase competitive pressure on co-occurring plant species during periods of extreme environmental changes (*Sphagnum fallax* during the climatic extreme summer of 2003, **Manuscript 2**), are significantly favoured by anthropogenic

acidification (Rochefort et al., 1990). Furthermore, *Sphagnum* species are well known ecosystem engineers, which can actively acidify their surrounding and, thus, change the environmental settings for other, co-occurring species (van Breemen, 1995; Bragazza, 2006). Based on the long-term monitoring of water chemistry and plant species composition of springs over 25 years we were able to detect strong positive feedbacks between historic acidification and biogenic habitat modification caused by *Sphagnum* species. These positive feedbacks showed significant effects on the long-term trajectories of plant community composition. Thus, ecosystem engineering *Sphagnum* species seem to maintain alternative states in plant species composition until today. Interactions between the abiotic environment and biotic system elements affecting the structure and, thus, functioning of ecosystems are major principles of complex adaptive systems theory. However, information about such kind of interactive processes is scarce for artificial experimental ecosystems and almost absent for natural ecosystems. With this study we therefore contribute to a general, integrative ecological understanding about path-dependence, abiotic-biotic interactions and alternative states of ecosystems. These findings are not only applicable for springs but transferable to other ecological systems.

Manuscript 5 aims at the scale-dependence and cross-scale interactions of abiotic environmental conditions and biotic response characteristics, which is proposed to be another major principle of complex adaptive systems theory in ecology. We therefore compared the relationship between the spatial occurrence of species inhabiting springs and the prevalent temperature regime, which is conceptualised in the species realised temperature niche, over seven orders of magnitude of spatial scale ranging from local (below metre) and regional (kilometre) scale to a continental scale covering several thousands of kilometres. Based on these cross-scale comparisons we observed a high degree of cross-scale similarity for the characteristics of the species temperature niches. Temperature optima, means the temperatures where the probability of species occurrence maximises, were similar for all tested species across the whole range of investigated spatial scale. However, the importance of temperature as abiotic driver of species occurrence decreased non-linearly with decreasing spatial scale. Thus, additional (biotic) drivers seem to be more important for species occurrence on small spatial (local) scales, whereas the importance of abiotic (climatic) drivers significantly increases with increasing spatial scale. Ecological processes and patterns are usually reported to be highly scale-dependent. High degrees of cross-scale similarity are rarely reported or even refused to exist in current literature (see Chapter 1.7.4). We argue that the high cross-scale similarity that is observed in this study for the realised temperature niche of species is mainly attributed to 1) high environmental stability, thus, low environmental noise, which is characteristic for springs at local scale and 2) strong cross-scale links between the environmental drivers affecting species occurrence on local scale and the abiotic drivers shaping species distribution on continental scale (for more details see Chapter 1.7.4). By contributing to the general understanding about cross-scale interactions and the scale-dependence of abiotic environmental conditions and species responses, this study will help to improve niche-base distribution modelling, which is currently the most widely used tool to asses climate change effects on species diversity but still neglects cross-scale interactions. We furthermore argue that the species realised niche might provide a simple ecological rule that can be used to conceive the complexity of ecosystem functioning across a wide range of scales.

Manuscript 6 addresses the methodological requirements of a sound description of ecological patterns, which is a prerequisite for testing and further developing ecological theories. When describing ecological patterns, ecologists commonly rely on statistical tests. However, dependent on the amount of environmental noise masking the focal pattern, ecological patterns might be invisible for statistical tests. Furthermore, common statistical measures like p-values or R^2 are very sensitive to sample size. Thus, small sample sizes can impede the statistical detection of an ecological pattern (type II error) whereas large sample sizes can lead to an erroneous, statistical detection of a non-existing pattern (type I error, for more detail see Chapter 1.8). By using artificial data with varying sample sizes, number of replications and amount of environmental noise, **Manuscript 6** provides the first technical guideline on how to optimally sample ecological gradients to maximize prediction success and to minimize the risk of lacking or false pattern detection. Based on the conducted simulations we show that the need of replication strongly increases with increasing random error but decreases with systematic errors. Thus, taking replicates is advisable for the study of controllable ecological systems with low amounts of 'hidden treatments' (c.f. Huston 1997), meaning low levels of additional confounding effects. This is normally the case for controlled manipulative ecological experiments or stable, natural ecosystems (see Chapter 1.3.2). However, when the chance of unaccounted, confounding effects is high like in many natural ecosystems the beneficiary value of replicates vanishes and then more emphasis should rather be put in more locations sampled along the gradient than into a higher number of replicates when the total number of samples is restricted due to restricted money, labour or time. In general, an increasing number of replicates decreased the risk of not detecting existing ecological patterns (type II error), which increased with increasing random noise. However, already moderate levels of systematic errors (additional confounding effects) strongly increased the risk of erroneous statistical detections of non-existing patterns. By providing the first fully reproducible technical recommendation about optimising ecological sampling, our study can facilitate appropriate and efficient sampling approaches and may help to reduce wrong conclusions drawn from spurious correlations. In consequence, our methodological contribution can help to reduce bias in the sampling and analyses an interpretation of ecological data that would significantly impede scientific progress (for more details see Chapter 1.8).

Table 2: Presentation of research related to this thesis at scientific conferences where I was the presenting author.

Date	Organisation	Conference and location	Title	Type
09/2013	Ecological Society of Germany, Austria and Switzerland (GfÖ)	43rd Annual Meeting: Building bridges in ecology, Potsdam, Germany	Springs as source of information for regional scale climate change effects	Oral
10/2013	Bayreuth Center of Ecology and Environmental Research (BayCEER)	BayCEER Workshop: Tracing the Life of Research Ideas, Bayreuth, Germany	AD FONTES for a better understanding of regional-scale climate change effects	Oral
01/2014	International Biogeography Society (IBS)	IBS Early Career Conference 2014, Canberra, Australia	Monitoring of helocrenic forest springs as a solution to the riddle of regional-scale climate change effects	Poster
05/2014	Society of Freshwater Science et al.	Joint Aquatic Science Meeting, Portland, Oregon, USA	Temperature and acidity regime as major driver of helocrenic plant community structure in Central Germany's lower mountain ranges	Oral, invited
09/2014	Deutsche Gesellschaft für Limnologie (DGL)	30th Annual Symposium: Leben in und mit dem Wasser, Magdeburg, Germany	Impacts of acidification and climate warming on helocrenic spring plant communities in Central Europe	Oral, invited
01/2015	International Biogeography Society (IBS)	7th International Conference, Bayreuth, Germany	How gradual warming, extreme weather and landscape interactively affects ecosystem processes	Poster
03/2015	COST Action ClimMani	ClimMani workshop on joint initiatives and common protocols in extreme events ecology, experiments and modelling, Copenhagen, Denmark	Optimizing sampling approaches along gradients	Oral, invited
07/2015	International Association for Vegetation Science (IAVS)	58th Annual Symposium: Understanding broad-scale vegetation patterns, Brno, Czech Republic	The legacy of a forgotten ecological disaster: Interactive ecological effects of 20th century acidification and climate change in central European spring fens	Oral

2.2 Outlook on emerging research challenges

Complex adaptive systems theory is a helpful but very general theory which can help to get a comprehensive picture of ecosystem functioning. To make this theory practicable and testable, one has to break it down into more applicable theoretical parts like the highlighted major principles. The five major principles discussed in this dissertation to be relevant for a more general understanding of ecosystem functioning were: 1) Diversity and organisation of biotic system elements; 2) Flow, distribution and interaction of information, energy and matter; 3) Stability and non-linearity of system reaction; 4) Scale-dependence and cross-scale similarity and 5) path-dependence of the system under study.

Springs were discussed to be ideal model ecosystems to test these major principles, as these ecosystems unite several advantages of experimental ecosystems (controllable environmental settings, defined boundaries) and complex, natural ecosystems like transboundary flow of information, energy and matter as well as abiotic and biotic cross-scale interactions and others (see Chapter 1.3.2). A comprehensive picture of ecosystem functioning has been designed in this thesis by integrating important theoretical concepts of ecology like the niche concept (sensu Hutchinson 1957), ecological resilience and elasticity (cf. Holling 1973), alternative stable states (Beisner et al. 2003) and the concept of scale (e.g. Levin 1992) into the framework of the complex adaptive systems theory. Based on this integrative approach, several pressing research questions directed to important knowledge gaps were identified. These will be discussed in the following.

The existence of fundamental ecological features

Complexity as a feature of ecological systems makes it hard or even impossible to examine every little detail of these systems (Levin 2002). However, complexity is argued by several authors to emerge from quite simple processes (Holling 1992, Bak 1996, Kauffmann 1996). Increasing empirical evidence suggests the existence of a small set of fundamental, ecological features regulating the functioning of entire ecosystems across a multitude of scales (Holling 1992, Peterson et al. 1998, Whittaker et al. 2001, Anderson & Mouillot 2007). The identification of such kind of fundamental ecological features might therefore help to improve our understanding of general ecosystem functioning by ignoring less important details (Levin 1992). One major requirement which has to be fulfilled by such fundamental features is scale invariance, meaning that these are able to explain ecosystem functioning irrespective of scale at least across the range of spatial and temporal scale that is relevant for ecological processes and pattern formation (Wiens 1989, Levin 1992, Levin 1999, Whittaker et al. 2001). Several attempts have been undertaken to identify scale invariant properties of ecological systems including scale response curves such as the species-area-relationship (Drakare et al. 2005) or the concept of fractal geometry (Mandelbrot 1982, Halley et al. 2004). In **Manuscript 5** we argue that the species realised niche might be such kind of scale invariant, fundamental ecological feature. We furthermore argue that the amount of environmental noise might be an important determining factor whether cross-scale similarity of ecological features like

the species realised niche is detectible or not. In other words, excessive environmental noise on small spatial scale can impede the identification of scale invariant, fundamental ecological features. Based on the observations we made for springs, my future research will elaborate in more detail on the scale-dependence of species realised niche characteristics and the underlying drivers. Therefore I plan to compare the degree cross-scale similarity of species niche characteristics for different ecosystems characterized by different amounts of small-scale noise as well as different degrees of cross-scale links among the driving environmental parameters (e.g. links between macro- and microclimatic conditions).

The role of contingency in explaining ecological patterns and processes

Contingency as a combination of randomness and the sensitivity to initial conditions is assumed to be a major cause of biotic heterogeneity in ecological systems across a wide range of spatial and temporal scales. Furthermore, contingency is proposed by Scheiner & Willig (2011) as an important conceptual part of a general theory of ecology. High amounts of contingency might blur fundamental ecological features and, thus, hamper a more general understanding of ecosystem functioning. Understanding the nature of contingency in ecological systems will therefore help to sort out regularities from randomness which is a major aim of complex system understanding (Gell-Mann 1994). One important question to ask addresses the nature of environmental noise.

Two types of noise are traditionally assumed to hamper the quantification and measurement of processes in ecological systems and, thus, influence the obtained data and the analyses and interpretations based on them (Richardson et al. 2012). Whereas random noise describes the variance induced by stochasticity, systematic noise accounts for mechanistic, thus, directional but unaccounted processes affecting the functioning and structure of ecosystems. Although these two kinds of environmental noise strongly differ in their ecological effects, they are hard to separate. Thus, questions and approaches tackling the isolation and the independent effect of these different types of environmental noise on ecological pattern formation and detection is crucial for a better understanding of ecosystem functioning. In **Manuscript 6** we provide the first, technical step forward in this direction by using artificial data. In my future research I plan to focus on 'real world' data to disentangle the contribution of stochasticity and directional noise in natural ecosystems. To pursue this aim, I will compare the statistical characteristics of different types of ecological data, which are assumed to be affected by different types of noise (e.g. abiotic vs. biotic data).

Furthermore, the role of stochasticity and determinism in shaping ecological systems is assumed to change with system development. Whereas young systems are assumed to be characterised by high levels of stochasticity, older systems are believed to be mainly characterised by deterministic processes (Margalef 1975). Furthermore, flexibility and stability of ecological systems are assumed to change with changing influence of stochasticity and determinism and, thus, will be modified with ongoing system development (Margalef 1975, Levin 1998, Holling 2001, Gunderson & Holling 2002). Young systems are thought to be characterised by high levels of stochasticity leading to high diversification and flexibility, whereas older systems are assumed to be driven by determinism leading to higher stability (Gunderson &

Holling 2002). Although these ideas are theoretically well-conceptualised and implemented in ecological sub-disciplines like succession research (e.g. Walker et al. 2010), empirical work on a general applicability of this theoretical concept outside of succession research like e.g. in an evolutionary context is lacking (but see Ward and Thornton 2000 for the colonisation of islands). In my future research career I plan to test the general applicability of these theoretically well-founded concepts.

The role of cross-scale interactions in explaining ecological patterns and processes

Scale-dependence is another important but still under-investigated factor determining the emergence and detection of ecological patterns and processes. Hereby the scale-dependence of ecological processes and patterns should not only be seen as a mechanistic explanation but rather as a stand-alone research subject onto which ecological research should be directed to deepen our theoretical understanding (Rahbek 2005, Beck et al. 2012). Instead of asking for the right scale of observation we should rather ask for the underlying mechanisms affecting the degree of scale-dependence (Thrush et al. 1997). In **Manuscript 5** we argue that the intensity of abiotic cross-scale interactions strongly controls the degree of cross-scale similarities observed for ecological features like the species realised niche. In other words, increasing cross-scale interactions of environmental conditions driving biotic responses seem to increase the similarity of these responses across scales. However, research on cross-scale interactions is largely lacking although theoretical concepts of emerging ecological research field like macrosystems ecology (Heffernan et al. 2014) strongly propagate this theoretical principle. Thus, cross-scale interactions and their effect on ecological structures and processes will be another point of my future research agenda. Hierarchically structured analyses based on the combination of ecological data from local-scale field investigations with information from airborne and satellite-based remote sensing might therefore provide a promising approach. A solid basis for this approach is provided by the recently launched ECOPOTENTIAL-Project, in which ecological information from field investigations and remote sensing approaches will be complied for protected areas all across Europe and beyond. Sampling grain, extent and lag that have to be adapted when combining data from different scales to study cross-scale interactions are thereby important facts to consider (Thrush et al. 1997).

The role of data quality in explaining ecological patterns and processes

Ecology as a discipline strongly focusing on the detection and interpretation of patterns in the noisy nature heavily relies on statistics when analysing the acquired data. Statistical analyses are accepted as seemingly sound methods to detect or prove the existence of ecological patterns (Prairie & Bird 1989). The primary role of statistics in ecology is to accomplish clarity and objectivity of detected ecological patterns (Hurlbert 1984). However, standard statistical methods and metrics used in ecological research have several shortfalls and methodological restrictions, which can lead to erroneous or completely wrong conclusions (see type I and type II error problematic in Chapter 1.8). Furthermore, increasing availability of data in modern world ecology bears the risk of overconfidence about the informative value of big

datasets (see Box 3). The overconfidence about the informative value of big datasets in combination with the problems big datasets cause in standard statistical methods and measures (see Chapter 1.8) have the potential to further aggravate the problem of misinterpretations and, thus, hamper scientific progress. This fundamental problem is widely ignored and guidelines for proper use and also for limitations of ecological statistics are missing. My further research activities will therefore focus on the effect of increasing data availability and, thus, increasing sample sizes on the risk to statistically detect patterns with less or no ecological significance. This problem of 'type I error inflation' caused by increasing sample sizes seems to be especially pressing for ecological sub-disciplines dealing with large amounts of data. To test these assumptions, I will combine simulations based on artificial data with a literature review about the statistical test results from different ecological sub-disciplines.

In **Manuscript 6** we show that replication in ecological sampling can help to overcome the problems related to a lacking statistical detection of existing patterns (type II error) or an erroneous detection of non-existing patterns (type I error) especially for high degrees of stochasticity. However, the 'hidden treatment effect' (c.f. Huston 1997) of additional confounding variables affecting the focal pattern in a systematic way but which is not accounted for in sampling design or analyses can easily lead to spurious inferences (c.f. Prairie & Bird 1989). This means that an erroneous, ecological causality is assumed based on a statistically significant relation between two tested variables when this is actually driven by not accounted, confounding factor(s).

Especially confounding factors, which are not recorded for during data collection and analyses and, therefore can cause 'pseudoreplication' (c.f. Hurlbert 1984) are commonly assumed to have significant, negative effects on ecological conclusions drawn from the results of statistical tests. Pseudoreplication is defined as the application of inferential statistics to test the effect of a certain factor, where sampled replications are assumed to be statistically independent but are actually not (Davies & Gray 2015). Statistical dependence of seemingly independent samples is thereby caused by not accounted, confounding variables. However, truly independent samples, which are prerequisites for standard statistical tests, are impossible to achieve in natural systems. There, everything is connected to everything else, at least to some degree. This makes the call to avoid pseudoreplication quite ambiguous. This unsolved dilemma is one reason for the intense but still unresolved debate about the effects of pseudoreplication on the interpretation of ecological studies (see Hurbert 1984, Oksanen 2001, Davies & Gray 2015). However, knowledge to which degree pseudoreplication as an inevitable property of natural systems affects the validity of commonly used statistics is missing up to now. In other words, the question is not whether pseudoreplication occurs in ecological sampling but to which degree of pseudoreplication the applied statistical tests are valid and significant. Thus, simulations using artificial data similar to the approach used in **Manuscript 6** can help to clarify the ambiguous concept of pseudoreplication and might therefore contribute to resolve the still continuous discussions.

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4 Declaration of own contribution to each manuscript

Manuscript 1:

Title: **Water temperature and acidity regime shape dominance and beta-diversity patterns in the plant communities of springs**

Authors: Schweiger, A. H.; Beierkuhnlein, C.

Journal and status: **Frontiers of Biogeography**, 6(3) (2014): 132-143, ISSN: 1948-6596

Personal contribution: idea and concept: 70%, data analysis and figures: 100%, writing: 90%, corresponding author

Manuscript 2:

Title: **The acid taste of climate change: 20th century acidification is re-emerging during a climatic extreme event**

Authors: Schweiger, A.H.; Audorff, V.; Beierkuhnlein, C.

Journal and status: **Ecosphere**, 6(6) (2015): 1-11, doi: 10.1890/ES15-00032.1

Personal contribution: idea and concept: 80%, data analysis and figures: 100%, writing: 90%, corresponding author

Manuscript 3:

Title: **Salt in the wound: The interfering effect of road salt on acidified forest catchments**

Authors: Schweiger, A.H.; Audorff, V.; Beierkuhnlein, C.

Journal and status: **Science of the Total Environment**, 532 (2015): 595-604, doi: 10.1016/j.scitotenv. 2015.06.034

Personal contribution: idea and concept: 85%, field work: 15% (550 working hours), data analysis and figures: 100%, writing: 90%, corresponding author

Manuscript 4:

Title: **The ecological legacy of 20th century acidification carried on by ecosystem engineers**

Authors: Schweiger, A. H.; Beierkuhnlein, C.

Journal and status: Submitted to **Applied Vegetation Science** as an invited contribution to the special feature on vegetation resurveys, under review, Manuscript ID: AVS-S-01682

Personal contribution: idea and concept: 85%, field work: 25% (210 working hours), data analysis and figures: 100%, writing: 90%, corresponding author

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Manuscript 5:

Title: **Scale-dependence of temperature as abiotic driver of species distribution**

Authors: Schweiger, A. H.; Beierkuhnlein, C.

Journal and status: Resubmitted to **Global Ecology and Biogeography**, under review, Manuscript ID: GEB-2015-0404.R1

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Manuscript 6:

Title: **Optimizing sampling approaches along ecological gradients**

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5 Manuscripts

5.1 Manuscript 1

Water temperature and acidity regime shape dominance and beta-diversity patterns in the plant communities of springs

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Abstract

The processes underlying species' dominance patterns and community composition are insufficiently investigated for springs, yet these systems, which are believed to be very stable environments, represent an important interface between aquatic and terrestrial habitats contributing significantly to local and regional diversity. We studied the dominance patterns and plant community composition of 238 springs in Central Europe. According to the conventional ecological belief we hypothesized (1) a positive relationship between local abundance and regional distribution of spring plant species, as well as between species commonness and species' realized breadth and (2) the occurrence of oligarchic species similar to other stable environments like tropical forests. Based on previous studies on these springs, we furthermore hypothesized (3) that water pH – essentially a proxy for nutrient availability – is the major driver of spatial compositional dissimilarity, i.e. beta-diversity. We tested these three hypotheses by using species commonness estimates, realized niche space and generalized dissimilarity modelling based on hydrochemistry. In line with conventional wisdom, we report a positive relationship between local abundance, species commonness and regional distribution for the majority of the species. In contradiction to other systems, we found both specialist and generalist species to be locally dominant and regionally widespread, thus common, while species with intermediate niche breadth showed the lowest commonness values. However, we detected three oligarchic species, exceeding all other species in local abundance and regional distribution, which did not follow these relationships. Both dominance relations (oligarchy) and community composition were mainly driven by water temperature and concentration of elements related to acidity regime (Al, Cd, Ca and Mg), although much of the variation in both remained unexplained. Thus, further research should focus on biotic interactions, which are likely to be important drivers of plant community composition in springs.

Keywords

beta-diversity, community composition, generalized dissimilarity modelling, helocrenic forest springs, hierarchical variation partitioning, niche space hyper volume, realized niche breadth, species commonness

Introduction

The organisation of ecological communities and ecosystems has been a central topic in ecology and biogeography for decades (Brown 1984, Condit et al. 2002, Legendre et al. 2005). The extent and direction of community responses to a changing environment in space and time strongly depend on the initial species composition, species cover and abundance (Grime et al. 2000, Potts et al. 2006). In general, communities consist of a set of interacting species, where relative success in the competition for resources shapes dominance relations within these communities (Whittaker 1965). Species are unequally successful, so natural communities are often characterized by a few species that repress other co-occurring species (Whittaker 1965, McNaughton and Wolf 1970). Whereas these species dominate in terms of structure and productivity, numerous additional species comprise the majority of species diversity (McNaughton and Wolf 1970).

Local abundance and spatial distribution have been shown, in numerous studies, to be intimately positively related (Brown 1984 and references therein, Gaston et al. 1997, Gregory and Gaston 2000). A high local abundance means a large number of individuals of a species at a given site (Gaston et al. 1997). Whereas most species are both rare and regionally restricted, a few species show local hyper-dominance and a wide regional distribution. We call these hyper-abundant, widespread species 'oligarchic species' (Pitman et al. 2001). The occurrence of oligarchic species, which is known for many tropical forests (Arellano et al. 2013), may be especially favoured by stable environmental conditions (Pitman et al. 2013). Several authors argue that oligarchic species occupy the widest ecological niches, leading to their local hyper-dominance and wide distribution (e.g., McNaughton and Wolf 1970, Brown 1984, Pitman et al. 2001). In contrast, species with narrow ecological niches might reach high local abundance under certain appropriate conditions but are commonly denied a wide spatial distribution (Pitman et al. 2013).

The realized niche of a given species is defined as a set of abiotic as well as biotic environmental parameters, which enable or limit the survival and reproduction of the species (Hutchinson 1957). Spatial variation in both abiotic conditions (e.g., climate or geology) and biotic conditions (including interspecific differences in dispersal ability, competitive strength and historical effects), drives patterns of compositional dissimilarity within a given type of ecosystem (Condit et al. 2002). This can be quantified as compositional dissimilarity between communities or beta-diversity (sensu Whittaker 1960, 1972). Although community composition and beta-diversity patterns have been popular subjects for ecologists and biogeographers for more than three decades, underlying processes and environmental drivers are still not entirely understood, and have been insufficiently investigated, in particular for less 'popular' systems like springs.

Despite their importance for clean water supply and local as well as regional biodiversity, springs are underrepresented in ecological research (Cantonati et al. 2012a, b). Springs are often very small ecosystems but at the same time very numerous, both regionally and globally (Glazier 2012). As an interface between aquatic and terrestrial habitats, springs harbour numerous specialized species which strongly respond to changes in water chemistry and thus the biogeochemistry of the catchments feeding them (Beierkuhnlein and Gollan 1999, Cantonati et al. 2006, Kapfer et al. 2012, Kubíková et al. 2012). Among all the morphological types of springs described by Thienemann (1924), 'helocrenic' springs

(seepage springs) host the most specialized and taxon-rich communities (Cantonati et al. 2012a). These springs are characterized by a spatially diffuse emergence of slow-flowing water, which causes a constantly water-saturated, swampy zone (seepage area) with a spatial extent of several to a few hundred square metres (Thienemann 1924, Cantonati et al. 2012a).

Most previous studies of springs focused on the zoological legacy of the groundwater (see Cantonati et al. 2012a for review). In consequence, springs are understudied in terms of plant communities, although they typically harbour an extraordinary diversity of specialized plant species in very small areas (Cantonati et al. 2006, Spitale et al. 2012). Studies of the plant community composition of springs are a prerequisite for understanding what determines the biodiversity and abundance patterns of these vulnerable systems.

In this study, we investigate the spatial patterns of dominance and beta-diversity of 238 helocrenic springs in the lower mountain ranges of Central Germany and the north-west Czech Republic. We focus on two research questions: (1) How are these spring plant communities organized in terms of species' local abundance and regional distribution? (2) What are the major environmental drivers of compositional dissimilarity and thus beta diversity patterns in these systems?

Pristine springs are commonly believed to be characterized by very stable environmental conditions (including water temperature, acidity regime and nutrient availability). We therefore hypothesized that the dominance patterns of spring plant communities should by characterized by oligarchic species, similar in this respect to tropical communities. We further hypothesized a positive relationship between local abundance and regional distribution of spring plant species, as well as between species commonness (as a combination of local abundance and regional distribution) and the volume of the species' realized niche. Based on previous studies about abiotic drivers of plant community composition (Audorff et al. 2011), we hypothesized that water pH (essentially a proxy for nutrient availability) is the major driver of spatial compositional dissimilarity.

Methods

Study region

We studied dominance relations and compositional dissimilarity of spring plant communities for 238 springs from five mountainous landscapes of east-central Germany and the north-west of the Czech Republic (Thüringer Schiefergebirge n=48 springs, Thüringer Wald n=41, Frankenwald n=50, Fichtelgebirge n=41 and Erzgebirge n=58, Fig. 1). The springs studied represent the helocrenic spring type (Thienemann 1924, Cantonati et al. 2012a), with continuously water-saturated seepage areas of a few to some hundred square metres. The individual discharge rates are mostly low (mean discharge = 0.3 L s^{-1}) but relatively constant throughout the year. Springs of this kind occur at high spatial density in the study region, allowing investigation of community responses at the landscape scale.

We chose predominantly forested catchment areas, mainly characterized by Norway spruce (*Picea abies*, L. H. Karst.) but also partly by European beech (*Fagus sylvatica*, L.). The altitude of the springs sampled ranges from 270 to 1240 m a.s.l. The climatic conditions are transitional between oceanic and continental climates. Detailed regional characteristics are provided in Audorff et al. (2011). The dense siliceous bedrock does not allow groundwater to penetrate. Instead, water is transported mainly as interflow close to the surface, in Pleistocene solifluction layers covering the whole area, which was not glaciated (Kleber et al. 1998). Thus, retention time of precipitated water in the catchments is rather short: a magnitude of weeks to months. Therefore, hydro-chemical spring water characteristics are expected to be directly coupled to biogeochemical processes in the catchments (Beierkuhnlein and Durka 1993).

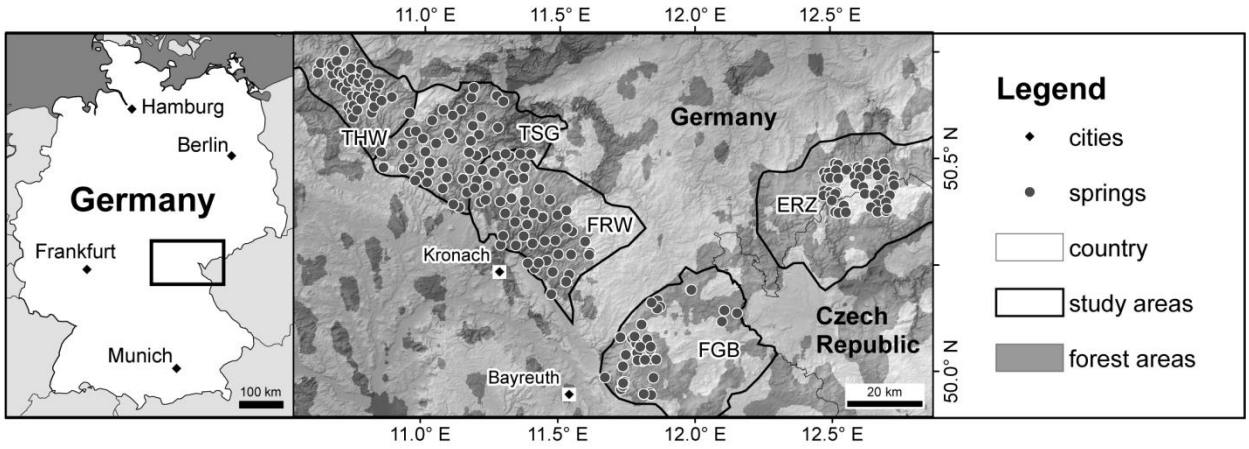

Figure 1. Locations of the helocrenic springs investigated in central Germany and the north-west Czech Republic (THW: Thüringer Wald, TSG: Thüringer Schiefergebirge, FRW: Frankenwald, FGB: Fichtelgebirge, ERZ: Erzgebirge).

Data collection

We investigated abundance/dominance relations of spring plant communities and hydro-chemical water characteristics for all springs between 1989 and 1996. For the vegetation surveys we determined all vascular plants, mosses and liverworts of the spring communities during July or August of the study years. Because previous studies on these springs have shown that bryophytes do not significantly differ from vascular plants in their response to interannual environmental changes (pH, electric conductivity, water temperature and discharge; Kapfer et al. 2012), we pooled all three groups for our study. As a result of seasonal frost heaving in winter, the helocrenic seepage area is well differentiated from the forest floor, which allows easy delimitation of the spring site from the surrounding area. We quantified local abundance of each plant species by estimating the cover using a modified Braun–Blanquet method (Reichelt and Willmanns 1973), where the Braun–Blanquet scores: r, +, 1, 2m, 2a, 2b, 3, 4 and 5 were transformed for analysis to mean percentage covers of: 0.01, 0.2, 2, 3, 10, 20, 37.5, 62.5 and 87.5, respectively.

Surveys of water hydro-chemistry took place in late September and October of the corresponding years. To avoid any kind of distorting effect caused by physico-chemical atmosphere–water interactions, we sampled spring water at the uppermost point of the seepage area with above-ground flow. We measured water temperature, electrical conductivity and pH in situ using a portable pH–conductivity multimeter with a liquid electrolyte pH-probe/conductivity probe (WTW pH/Cond 340i with WTW SenTix 81/WTW Tetra- Con 325, Wissenschaftlich-Technische Werkstaetten GmbH, Weilheim, Germany). Because water temperature of springs is very stable at least within a timeframe of hours to days, we did not account for the time differences between the different measurements at the different spring sites. We visually estimated water discharge based on a seven-point ordinal scale, ranging from 0 to >1.5 L s^{-1}. We determined acid neutralisation capacity (ANC) in the laboratory using titration (0.01 M HCl to pH 4.3). Concentrations of nutrient and toxic elements / compounds (Ca, K, As, B, Be, Ba, Co, Cr, Cu, Fe, Hg, Mo, Ni, NO_3, SO_4, PO_4, NH_4, DOC, Al, Pb, Se) were determined *ex situ* in the laboratory using filtered (0.45 µm cellulose acetate filters, Satorius Stedim Biotech GmbH, Goettingen, Germany) and partly acidified (HNO_3, distilled) water samples. Additionally, we quantified light regime at the particular spring site by estimating the percentage tree cover. Elevations of the spring sites were derived from a digital elevation model. Subsequently, we used this set of 36 environmental variables to quantify species' realized niche breadth and compositional dissimilarity.

Data analyses

We quantified species' commonness as a parameter representing both local abundance and spatial frequency of occurrence, based on the h-index of academic productivity, using the r-command provided by Arellano et al. (2013). For each species, a proportional index (h_p) was assigned when the species was present in h_p percentage of the 238 spring sites with h_p percentage or more cover in each of the studied spring sites (for details see Arellano et al. 2013). Afterwards, we divided all the h_p-indices by the maximum h_p-index observed among the considered species. We used this relative h-index to quantify the commonness of the spring plant species. Based on their calculated commonness values, we categorized all species into three groups: oligarchic, common and rare species, following Arellano et al. (2013). Common species were separated from rare species based on the intersection of the x=y (1:1) line with the proportional commonness–rank curve (see Fig. 2). Therefore we used the commonness-value (y-value, h_h in Fig. 2) of this intersection as a threshold to separate common (>h_h) from rare species (≤ h_h; see Arellano et al. 2013).

Furthermore, we quantified the extent of each species' realized niche space. To ensure statistically robust niche space estimates, we only considered species occurring in more than 50 springs. Our definition of niche space followed Hutchinson (1957), who defined a species niche as an n-dimensional hyper-volume of environmental characteristics in which the species/population can maintain a positive net growth rate. To calculate the Hutchinsonian hypervolume of individual niche spaces we conducted kernel-density estimations based on relevant environmental variables ('hypervolume' package for R, v.0.9.9.7, Blonder 2014). Relevant environmental variables were selected based on knowledge from previous studies

conducted in this region about the environmental drivers of spring plant community composition (Audorff et al. 2011, Kapfer et al. 2012) and spatial coverage (available for more than 75% of all springs). Thus, a set of 16 environmental variables was used: elevation, water temperature, discharge, pH, electric conductivity, ANC as well as the concentrations of K, Na, Ca, Mg, Cd, Mn, Al, NO_3, SO_4, PO_4 and NH_4. To reduce the number of dimensions and to minimize distorting effects caused by co-linearity between the variables we *a priori* performed a principal components analysis (PCA) based on all 16 variables. To quantify the species' Hutchinsonian hypervolume we used the first three PCA axes, which accounted for more than 99.9% of the total variation.

Additionally, we analyzed the effect of abiotic environmental conditions on compositional dissimilarity by using generalized dissimilarity modelling (Ferrier et al. 2007). This statistical technique, which can be used to analyse and predict beta-diversity patterns across large spatial scales, is an extension of matrix regression, which is capable of handling non-linearity in large-scale ecological datasets. We included geographical distance between sites (Euclidean distance based on spring site coordinates) as an additional term in the model. We quantified compositional dissimilarity by calculating the Bray–Curtis dissimilarity between all investigated communities/springs. Dissimilarities between the spring plant communities were modelled by the abiotic variables based on I-spline basis function fits to the environmental predictors in combination with a maximum-likelihood estimation of model coefficients. We used the percentage of deviance accounted for by the fitted model as a goodness-of-fit estimate. We selected relevant environmental variables, a subset of the 16 variables mentioned above, *a priori* by a stepwise forward and backward model approach. For both approaches, addition or removal of variables was stopped when percentage of explained deviance decreased after a maximum was reached. The final set of relevant environmental variables was selected by considering both forward and backward model selection. Based on these selection criteria, a set of 10 environmental variables was used for the analysis: water temperature, ANC as well as concentrations of Al, Mn, Ca, Mg, Cd, PO_4, NH_4 and NO_3. As we were particularly interested in the relative importance of single variables in explaining species composition we did not use the previously mentioned principle components which can be used to avoid co-linearity among the variables under consideration, although we detected moderate co-linearity among the chosen variables. We quantified the relative importance of the selected environmental variables in terms of accounting for the compositional dissimilarity between the investigated springs, using the hierarchical partitioning approach of Chevan and Sutherland (1991). This approach is considered adequate to quantify relative importance of single variables for non-linear models (Murray and Conner 2009). The goodness-of-fit measure was percentage of explained deviance and not R^2 (which is implemented in the hier.part R package v.1.0-4; Walsh and Mac Nally 2013), so we had to adjust the algorithms to our approach. We conducted all analyses in the R environment (v.3.0.2, R Development Core Team 2013) with the add-on package vegan (v.2.0-10; Oksanen et al. 2013). Generalized dissimilarity modelling was performed using the GDM R Distribution Pack (v.1.1, available at https://sites.google.com/site/gdmsoftware/, last accessed 18/09/2014). We conducted all analysis based on inferential statistics with a level of significance of $\alpha = 0.05$.

Results

Dominance relations

Species' commonness varied greatly; only 34 (20%) of the species were classified as 'common' (including the three oligarchic species, see Fig. 2), the rest as 'rare' (133 species). We classified the herbaceous species *Chrysosplenium oppositifolium* L. and *Calamagrostis villosa* (Chaix ex Vill.) J. F. Gmel. and the moss *Sphagnum fallax* H. Klinggr. as 'oligarchic species'. All three species had considerably higher commonness values (> 0.7) than the other common species.

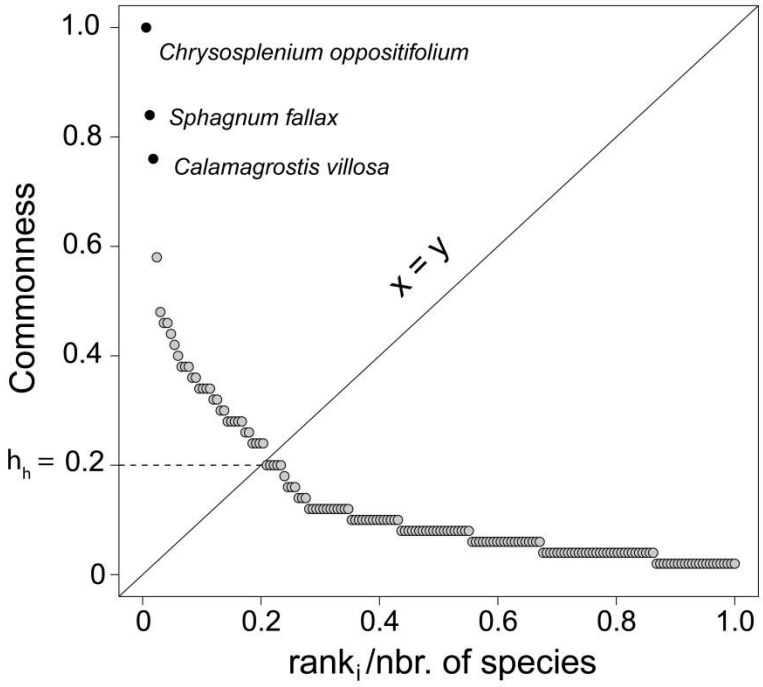

Figure 2. Commonness of helocrenic spring plant species in Central Europe. Commonness is measured as proportional commonness based on the commonness value of the most common species. Species are sorted by commonness (horizontal axis). Common and rare species are separated at $h_h = 0.2$ (see Methods). The three 'oligarchic species' are highlighted by black points and named.

We found a significant positive relationship between extent of spatial distribution (frequency of occurrence) and mean local abundance of the spring-inhabiting species, expressed as the arithmetic mean of species cover classes (Fig. 3a). We also found a significant positive relationship between extent of distribution and commonness (Fig. 3b). However, the three oligarchic species showed much higher local abundance (and thus commonness) than expected from their extent of distribution on the basis of the other species (see black points in Fig. 3).

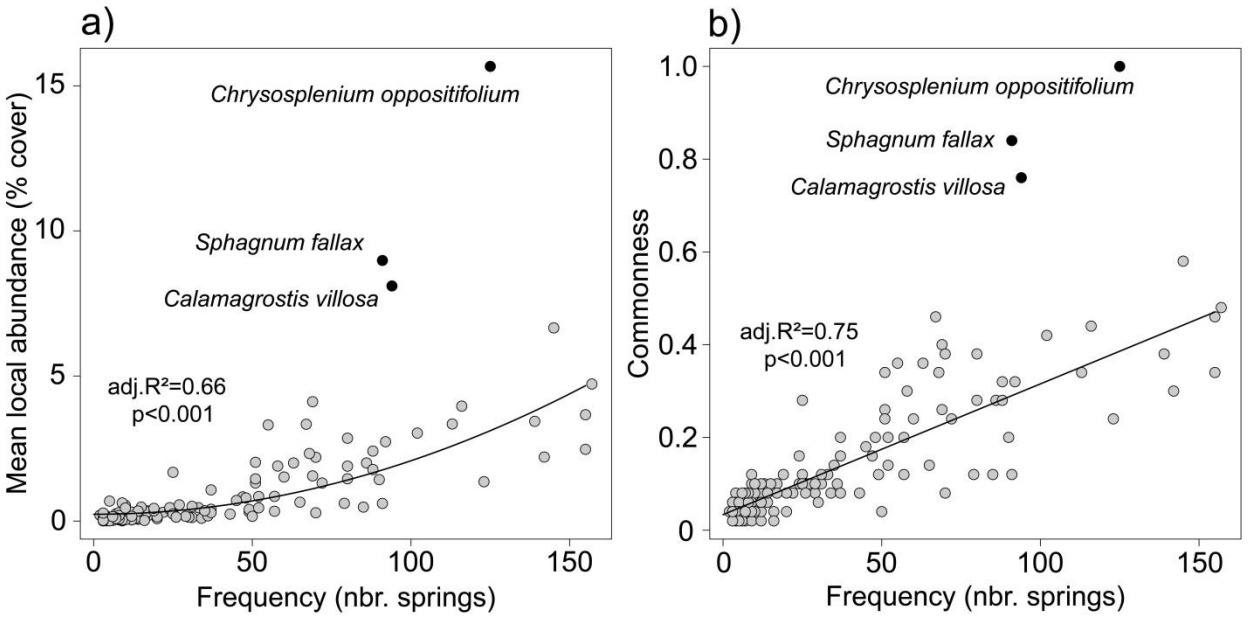

Figure 3. Relationship between species' spatial distribution, quantified by the number of occupied springs, and (a) mean local abundance, i.e. mean local cover, and (b) commonness of helocrenic spring plant species in Central Europe. The three oligarchic species are highlighted by black points and were not included in the regression models.

Species' realized niche breadth

Excluding the three oligarchic species, we observed a weak U-shaped relationship between species' niche volume and commonness (Fig. 4). The lowest commonness values were associated with intermediate niche volumes, with commonness increasing for both smaller and larger niche volumes. The three oligarchic plant species, *Chrysosplenium oppositifolium*, *Sphagnum fallax* and *Calamagrostis villosa* were again far removed from the main trend. Neither local abundance nor the extent of distribution were significantly related to realized niche breadth.

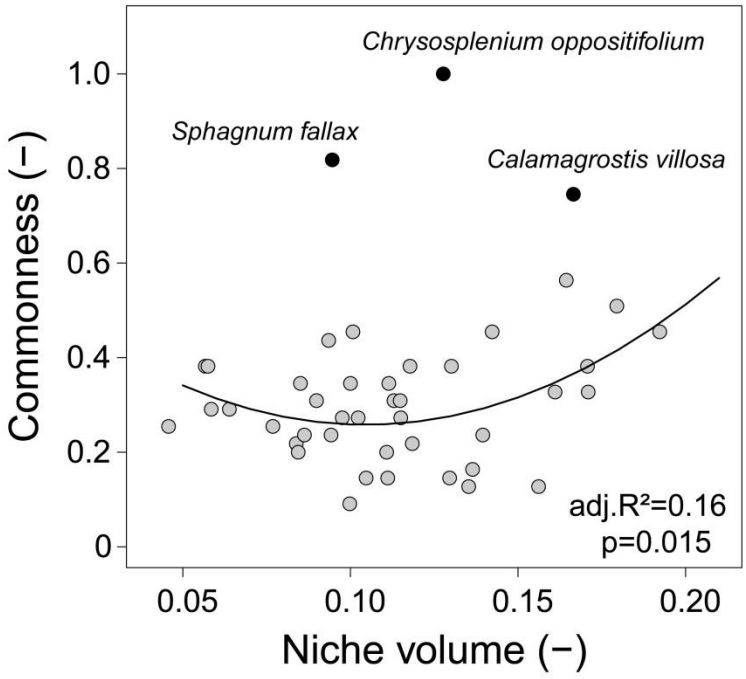

Figure 4. Relation between species' commonness and the volume of the realized ecological niche for helocrenic spring plant species in Central Europe. The three oligarchic species are highlighted by black points and were not included in the regression model.

Compositional dissimilarity

Using the 10 environmental variables selected *a priori*, and geographic distance as co-variable, we could account for 35.5% of the total deviance in compositional dissimilarity (Fig. 5a). Aluminium concentration and water temperature had the highest explanatory power (independent effects: 17.1% and 16.2% of total explained deviance, respectively; Fig. 5b). Element concentrations of Mn, Ca, Mg and Cd showed relative importance (independent effects) between 12.6% and 9.1%. Concentrations of nitrate, phosphate and ammonium, as well as acid neutralisation capacity (ANC), showed low relative importance (between 6.1% and 4.9%). Geographic distance considered as an explanatory variable showed a relative importance of 7.1% of total explained deviance.

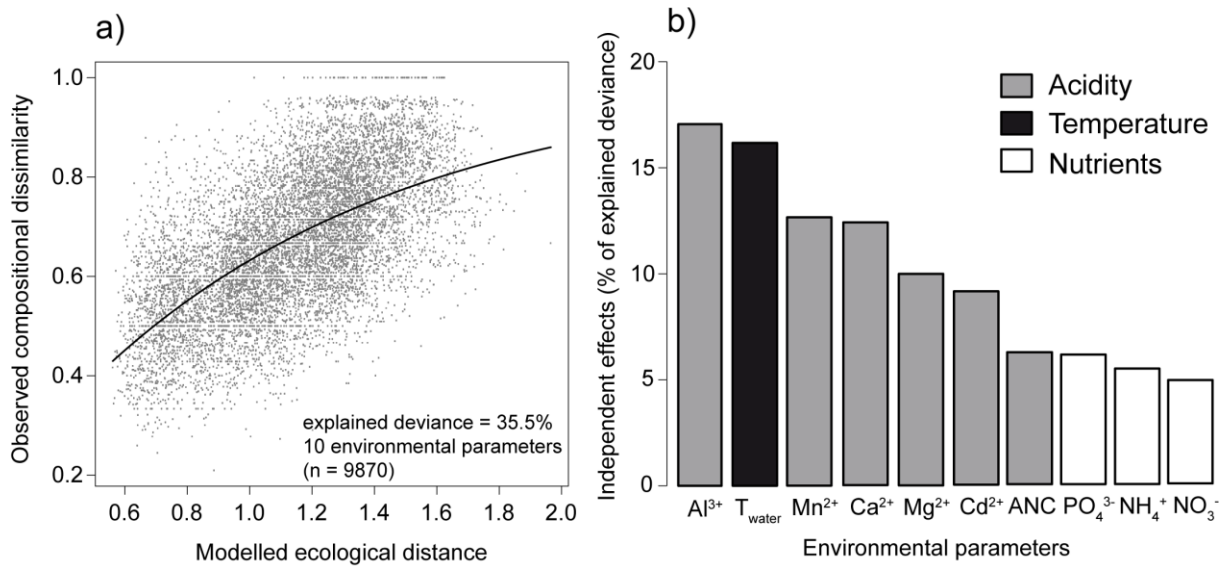

Figure 5. Abiotic environmental drivers of compositional dissimilarities between the helocrenic spring plant communities. a) Generalized dissimilarity model (gdm) fit between observed compositional dissimilarity and modelled ecological distance. Each point represents a pairwise comparison between springs. b) Relative importance (independent effects) of the 10 most influential environmental variables (based on hierarchical variation partitioning applied to the gdm). Different colours represent different groups of variables (black: temperature regime, grey: acidity regime, white: nutrient availability).

Increasing geographic distance among the spring sites promoted compositional dissimilarity in a largely linear manner (Fig. 6a). Increase in water temperature had minimal independent effects on the dissimilarity in community composition for lower water temperatures (below 8°C), but its effect increased rapidly with temperatures above this value (Fig. 6a). Environmental variables associated with the acidity regime of the springs affected compositional dissimilarity in a similar fashion to each other (Fig. 6b, c): we observed strong independent effects of ANC when this was low (below 0.1 mmol L^{-1}), and the same for concentrations of Ca, Mg and the heavy metal Cd (below 7.0 mg L-1, 2.0 mg L^{-1}, 0.1 µg L^{-1}, respectively). However, increasing values of these variables above these levels were associated with minimal additional effects. We found no such saturation in the independent effects of increasing concentrations of Al and Mn (Fig. 6c), both of which showed monotonic, decelerating effects; the overall effect size was smaller for Mn than for Al. Chemical compounds associated with the nutrient regime of the springs showed relatively small independent effects on compositional dissimilarity (Fig. 6d), with saturation behaviour for NH_4 and PO_4. The independent effect of increasing concentrations of NO_3 showed striking similarities to the effect size behaviour of water temperature and was more prominent than for the other two nutrient compounds.

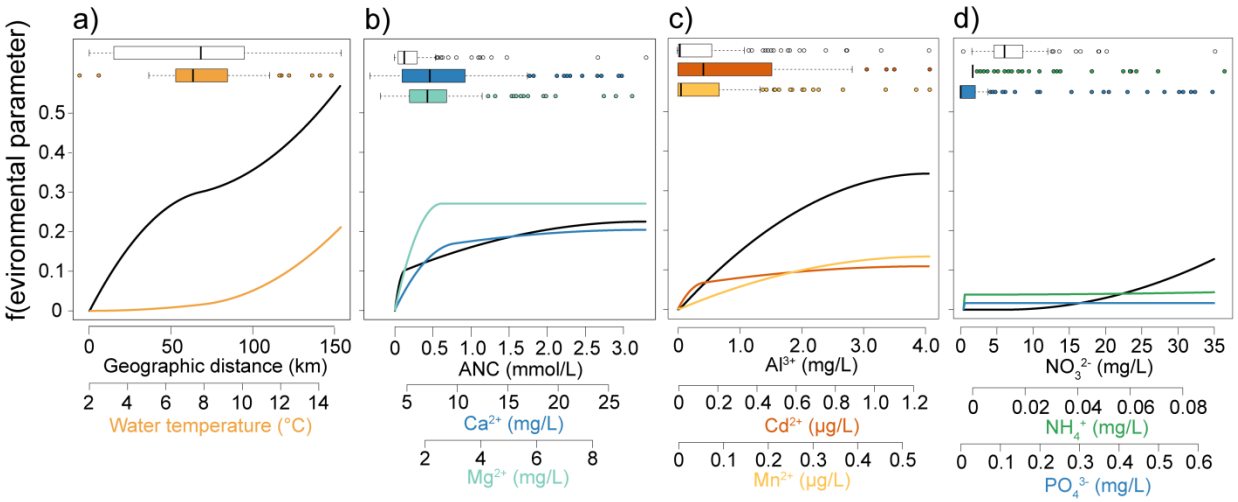

Figure 6. Effects of the 10 most influential abiotic drivers of compositional dissimilarities between the helocrenic spring plant communities. a) Geography and water temperature, b) and c) variables associated with acidification, d) nutrient elements. The slope and total values of each function (vertical axis) depict the rate and amount of compositional turnover, which is associated with the gradient of each environmental variable by holding all other parameters constant. Distributions of the measured values along the total gradient of each variable on which the fits are based, are depicted as boxplots correspondingly coloured in the upper part of the plots (box: first quartile, median and third quartile, whiskers: 1.5 times interquartile distance, points: individual values outside the whiskers).

Discussion

We found that oligarchic species, often associated with environmentally stable ecosystems like tropical forests (Arellano et al. 2013, Pitman et al. 2001, 2013), also characterize Central European spring plant communities. In support of the conventional belief in ecological literature (e.g., Gregory and Gaston 2000), we also found positive relationships between local abundance, species commonness and regional distribution for the majority of the species analysed. However, the three oligarchic species were strikingly different from all other species, with much higher local abundance; they did not follow the relationships we found between local abundance, regional distribution and commonness for the other species.

In general, two mechanisms have been proposed to explain positive relationships between local abundance and regional distribution: meta-population dynamics and differences in species' niche breadth. Regarding the first mechanism, species-specific differences in extinction and colonization rate (carrying capacity) are assumed to cause the positive relationship between local abundance and regional distribution, which shapes the meta-population structure. Following the carrying capacity hypothesis (Nee et al. 1991) locally abundant species are assumed to have lower extinction and/or higher colonization rates and, thus, are more widespread, especially when extinction events are frequent among meta- populations. As extinction events can be considered very rare in spring ecosystems (because of the very stable abiotic conditions), we assume this first mechanism to be negligible for spring plant communities. Regarding the second mechanism (niche breadth), it is argued that more abundant and widespread species can use a broader range of resources and, thus, have broader realized niches (McNaughton and Wolf 1970, Brown

1984). This would mean that oligarchic species occupy the widest ecological niches, leading to their local dominance and wide distribution (Pitman et al. 2001). This was not the case for our spring plant communities: the niche spaces occupied by the oligarchic species were intermediate compared with the co-occurring species. Furthermore, we found no linear increase of species' commonness with increasing realized niche space but rather a weak U-shaped relationship for the non-oligarchic species (and no relationship if the oligarchic species were included). In other words, non-oligarchic species with intermediate niche breadth were least common in the spring plant communities, whereas species with relatively narrow or wide niches were slightly more common.

Although a positive relationship between niche breadth and commonness can be inferred from theoretical models, various studies have failed to find any such relationship, or have found negative relationships (see Gaston et al. 1997 for review). According to Gaston et al. (1997) the main reason for this inconsistency is that most studies do not cover a spatial extent which is appropriate to cover the full range of environmental conditions under which species occur in a certain system. As a consequence most studies are not able to correctly determine species' realized niches. Furthermore, considering species that co-occur in the same system but have quite distinctive ecological characteristics and, thus, might occur in the same system but because of different reasons, might also lead to wrong conclusions (Gaston et al. 1997). We argue that neither problem affects our study. Although our study is confined to a regional scale, the narrow amplitude of environmental conditions characterizing the studied springs allowed us to cover the full range of environmental conditions under which the species occur in these systems. Furthermore, most spring plant species are specialized to the stable environmental conditions that characterize these systems and, thus, show quite similar ecological characteristics (Cantonati et al. 2012a). This quite narrow amplitude of environmental conditions to which species are especially adapted is not regionally restricted but characterizes springs of this type over large geographical extents. This may allow species with narrow ecological niches not only to reach high local abundance under certain, appropriate conditions (Pitman et al. 2013) but also to have wide regional distributions, causing the high commonness values we observed for these specialized species. So the common assumption, that generalist species will be more widespread than specialized species, seems only partly true for springs, where abiotic conditions are very similar and stable on long time scales and relatively large spatial scales. Thus, specialists with narrow ecological niches seem not to be disadvantaged compared to species with wider ecological niches.

Abiotic environmental conditions are commonly considered to shape dominance relations among co-existing plant species, and thus plant community structure (Ellenberg and Leuschner 2010). Consulting the extensive amount of phytosociological work which was done for the studied springs during the 1990's, all three oligarchic species we detected in our study clearly reflect the predominant environmental gradients of the springs, which are characterized by acidity (modern acidification and/or historic precipitation regime) and water temperature (elevation). The perennial *Chrysosplenium oppositifolium* is known to characterize neutral springs whereas the moss *Sphagnum fallax* characterizes acidified springs in the studied region (Audorff et al. 1999, Beierkuhnlein 1999, Beierkuhnlein and Schmidt 1999, Peintinger and Beierkunhnlein 1999, Riedel and Beierkuhnlein 1999). *Calamagrostis villosa* is a typical species of helocrenic springs in the cooler, higher elevations of this region above 700 m a.s.l. (Audorff et al. 1999). In a previous study of the environmental parameters shaping spring plant community composition in this

region (Audorff et al. 2011), hydrochemical variables related to the acidity regime (Al, Cd, Mn, Ca and Mg) played a fundamental role while spatial and hydrophysical variables (e.g., water temperature) were less important. Spring water chemistry, especially variables related to acidity and nutrient availability, has been shown in numerous studies to strongly affect plant community composition in Central European springs (Beierkuhnlein 1994, Hájek et al. 2002, Hájková and Hájek 2003, Hájková et al. 2004, 2008, Cantonati et al. 2012a). Furthermore, water temperature is known from several studies on benthic pro- and eukaryotic algae, diatoms and invertebrates to shape spring community structure (Cantonati et al. 2012b, 2012c, Glazier 2012). However, the actual shape of community response to abiotic factors has not been considered so far.

In our study, we can confirm the importance of temperature and acidity regime in shaping spring plant communities in Central Europe. Compositional dissimilarity between the springs was best explained by water temperature and concentrations of elements related to the actual acidity regime (Al, Mn, Cd, Ca, Mg). Although we observed a small effect of water temperature below 8°C, effect size increased strongly with increasing temperature. Low temperatures are known to limit the metabolic rates and, thus, the competitive ability of species (Brown et al. 2004). With increasing temperatures, species' metabolic rates are no longer limited, which might enhance competition among species and, thus, cause higher rates of community turnover (Glazier 2012). This seems to be especially the case for spring plant communities, where compositional dissimilarity between the different sites, and thus spatial community turnover, is strongly affected by temperature regime.

For the heavy metals Al and Mn, we observed increasing community responses over the full range of observed element concentrations. Both elements are known to be toxic for plants at high concentrations. Species' susceptibility to Mn clearly depends on the acidity regime prevalent at the site (Mahmoud and Grime 1977). The occurrences of species along a pH gradient also strongly depend on their Al tolerance. Among all elements affected in solubility by acidification, Al is one of the most cytotoxic, and thus most restricting, factors in terms of species' establishment and occurrence (Cantonati et al. 2006, Abedi et al. 2013). Although the bioactive concentrations of both elements are driven by the present acidity regime of the spring sites (Audorff et al. 2011), element concentrations rather than acidity itself (meaning the activity of H^+ ions) influence species' performance and, thus, drive the compositional dissimilarity between the springs. This indirect effect of acidity regime on spring plant community composition is confirmed by the high independent effects of Ca, Mg and Cd. Although all three elements are strongly affected by the prevalent acidity regime of the catchment/spring (Hruška et al. 2002), independent effects were visibly higher than the explanatory power of acidity itself (quantified as pH and ANC).

In this study we can support the notion that acidity and temperature regime are the predominant environmental factors directly and indirectly shaping plant community composition of Central European helocrenic springs. Considering the 10 most relevant environmental variables, we were able to account for 35.5% of the total variation in compositional dissimilarity. This exceeds the overall explanatory power which was reported by Audorff et al. (2011). By analysing springs from the same region but using a different analytical approach (partial correspondence analyses and multiple response permutation procedure) they were only able to account for 18.8% of total variation in spring plant community

composition using 18 abiotic variables. Reporting similar low predictive power of abiotic variables in explaining spatial variation in spring community composition (<17% of total variation), Spitale et al. (2012) assumed biotic interactions to be more important than generally perceived for these systems. Furthermore, neutral processes like interspecific differences in dispersal ability, which clearly depend on the geographic distance between the different spring sites, could account for the large portion of unexplained variation in compositional dissimilarity (Audorff et al. 2011). Although the importance of geographic distance in explaining community composition between the spring sites was higher than in the study of Audorff et al. (2011) (7.1% vs. 3.6% of total variation), this obviously important factor cannot account for the large portion of unexplained variation. Thus, unaccounted-for biotic interactions more than neutral processes are likely to be the reason for the relatively large portion of unexplained variation of compositional dissimilarity.

Conclusions

Understanding the patterns and underlying drivers of dominance relations and beta-diversity patterns of plant communities is one fundamental goal in ecology and badly needed to adequately assess future climate change effects on biodiversity and ecosystem functioning. This is especially relevant for springs, which house numerous species that are especially susceptible to a changing environment (e.g., climate change, acid rain) but are still underrepresented in ecological research. In this study we showed that species with narrow ecological niches, which are known from other systems to be locally dominant only under certain environmental conditions and, thus, restricted in regional distribution, are regionally widely distributed in springs. We also showed that oligarchic patterns in community composition occur in these helocrenic springs. Both circumstances seem to be caused by the relatively stable environmental conditions that characterize these semi-aquatic systems. Furthermore, we showed that water temperature (linked to elevation) and acidity regime (representing a combination of acidic deposition and bedrock traits), are major drivers of dominance relations and compositional dissimilarity between helocrenic spring plant communities in Central Europe. By identifying the patterns and important environmental drivers, we filled some of the important knowledge gaps regarding these understudied systems. However, further research should unravel in more detail the biotic interactions and responses to changing abiotic conditions which are projected for the future.

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5.2 Manuscript 2

The acid taste of climate change: 20th century acidification is re-emerging during a climatic extreme event

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Abstract

The current state of an ecosystem results from the complex interaction of abiotic and biotic drivers jointly influenced by their dynamics and the legacy of a systems' history. Negative synergies between emerging climatically extreme events and past environmental impacts are expected to shift ecological communities to alternative stable states or towards hysteretic successional trajectories. However, knowledge on mutual effects of environmental stressors is scarce especially for not experimentally controlled, natural ecosystems.

We investigated the effect of a prolonged drought and heat wave occurred during 2003 on the short-term vegetation responses of forest springs, a waterlogged type of ecosystem which is highly abundant in Central European siliceous mountains. These landscapes experienced strong impairment by 20th century atmospheric acidification. For different levels of acidification, we investigated plant community composition and water chemistry of 57 springs before (1996) during (2003) and after (2004–2006) the summer of 2003 and quantified ecological resilience and elasticity related to this extreme event for single plant species and species assemblages of whole communities.

The extreme dry and hot summer 2003 significantly decreased discharge, increased water temperature and affected water chemistry of the investigated springs. Ecological resilience and elasticity against the climatic extreme event differed significantly between communities dependent on their previous impact by acidification. Springs which were less affected by acidification performed higher resilience and elasticity than strongly acidified springs.

Our study shows that strong negative synergies between emerging climatic extreme events and past environmental impairments occur on landscape scale. Hitherto, such interactions between climate change, hydrochemistry, and the responses of ecosystems have been neglected.

Key words

climate change modelling; crenal habitats; ecosystem stability; extreme weather events; heat spell; insurance hypothesis; summer drought; response diversity; tipping point.

Introduction

A multitude of abiotic and biotic non-linear dynamics and interactions modified by historical events qualify ecosystems to be complex adaptive systems (Gell-Mann 1994, Levin 1998, Norberg 2004). One major aim in ecology is to increase the basic understanding and, thus, establish a proper concept of ecosystems by quantifying the characteristics and drivers of these complex dynamics (Potts et al. 2006). Although complexity is inherent in every ecosystem and complex ecosystem dynamics are a major topic in experimental ecology since the introduction of this concept (Standish et al. 2014), the interaction between abiotic triggers and biotic community response remains rarely studied for uncontrolled, natural systems.

Strong temporal dynamics in ecological communities are triggered by disturbances, discrete events in time which change abiotic environmental conditions and significantly disrupt ecological community structure (Picket and White 1985, White and Jentsch 2001). The temporal response of an ecological community to a certain disturbance can be simplified in a two dimensional model characterized by ecological resilience and elasticity (cf. Holling 1973). Whereas elasticity quantifies the ability of an ecosystem to return to a stable state after disturbance (Grimm and Wissel 1997), ecological resilience defines the amount of disturbance an ecosystem can absorb without changing its actual state (Holling 1973, Gunderson 2000).

During the last three decades of research, climate change is reported to have strong detrimental ecological effects on species, communities and ecosystems (Walther et al. 2002, Bonan 2008). But still, gradual shifts in temperature are in the main focus of climate change research. However, anthropogenically enhanced climatic variability and occurrence of extreme climatic events like heavy rainfall events or severe and extensive droughts that dramatically increased in frequency and severity in recent years (Ciais et al. 2005, Reichstein et al. 2007) are now widely recognized to be more disruptive in terms of ecosystem functioning (Jentsch and Beierkuhnlein 2008, IPCC 2014).

An extreme heat wave combined with a severe drought descended on large parts of Europe during the summer of 2003, with July temperatures exceeding long-term means by up to 6°C, combined with severe droughts expressed in annual precipitation deficits up to 300 mm $year^{-1}$, which were 50% below the long-term average (Luterbacher et al. 2004, Ciais et al. 2005). Such climatic events like in 2003 are expected to interactively cause strong adverse ecological effects with other stressors like historical environmental pollution (Lovejoy and Hannah 2005, Brook et al. 2008, Fordham and Brook 2010). However, such kind of mutual interactions between historical and emerging environmental stressors can hardly be accounted for in experimental studies and are difficult to identify in most terrestrial ecosystems (Heino et al. 2009).

Forest springs exhibit the advantage of low human disturbance in combination with a close relation between site conditions and species assemblages. Plant communities of springs are assumed to be especially susceptible to climatic extreme events like extensive droughts (Smith and Wood 2002, Wood et al. 2010) as these hybrid ecosystems linking groundwater to the upper-most section of surface running waters are commonly reported to exhibit very constant abiotic environments in terms of discharge,

temperature and water chemistry to which species are evolutionary adapted to (Odum 1971, van der Kamp 1995, Cantonati et al. 2006, Gerecke et al. 2011). As springs occur in a high spatial frequency in the mountainous regions of Central Europe they provide a unique study system to assess ecological effects of climatic extreme events on landscape scale by taking into account the full range of natural system complexity.

In this study we take advantage of the outstanding climatic event during 2003 to examine the effects of abrupt environmental changes on the response characteristics of single species and whole communities of central European forest springs (helocrenic springs sensu Thienemann 1924). Among all morphological types of springs theses springs host the most specialized and taxon-rich communities (Cantonati et al. 2012). Numerous studies on this type of springs showed that inhabiting plant species strongly respond to changes in water temperature and water chemistry and, thus, energetic and chemical shifts in their catchments (Kraeuchi 1993, Beierkuhnlein and Gollan 1999, Cantonati et al. 2006, Hájková et al. 2008, Audorff et al. 2011, Kubíková et al. 2012, Schweiger and Beierkuhnlein 2014). But still the multifarious effects of anthropogenic climate change in these complex, natural systems are neglected.

As the outstanding heat wave combined with a severe drought certainly affected water dependent communities (Zwolsman and van Bokhoven 2007), we expect strong and lasting effects on single species occurrence and whole plant community composition in the surveyed springs. Based on the assumed evolutionary adaptation of spring communities to long-term environmental stability we hypothesize low ecological resilience and elasticity to this extreme climatic event as well for single species as for whole plant communities.

METHODS

Study sites

The studied springs (n = 57) are located in the lower mountain ranges of Central Germany (latitude 49.9–50.68°N, longitude 11.2–12.28°E) and were strongly exposed to the heat wave and the severe drought (see Fig. 1A) which occurred during summer and autumn of 2003 (Schaer et al. 2004). All springs are fed by surface-near run-off (interflow) which leads to constant but rather low discharge rates mainly below 2 L/s.

The parent material in the catchments is characterized by siliceous bedrock (schists and granite), which causes the low buffering capacity against acidification and nutrient load of these springs under pristine conditions. The predominantly forested catchments are characterized by Norway spruce (*Picea abies* (L.) H. Karst), intermixed and only partly substituted by European beech (*Fagus sylvatica* L.) (further details see Audorff et al. 2011, Schweiger and Beierkuhnlein 2014).

Caused by the low buffering capacity in combination with high loads of acidifying pollutants all investigated springs/catchments were strongly affected by acidification caused by the unfiltered emission of acidifying pollutants, which culminated in the 1970s and 1980s (Matzner and Murach 1995). Since then, impact and effects of former acidification have slowly decreased but are still effective.

The year 2003 featured an extraordinary climatic situation in Central Europe. Precipitation deficits in combination with an early greening of vegetation in springtime caused high losses of soil moisture during spring which significantly intensified drought during summer of this climatically very extreme year (Fischer et al. 2007). The subsequent extreme drought period caused a decline in carbon sequestration at continental scale (Ciais et al. 2005). The discharge and even water quality of Central European rivers was therefore significantly affected (Zwolsman and van Bokhoven 2007).

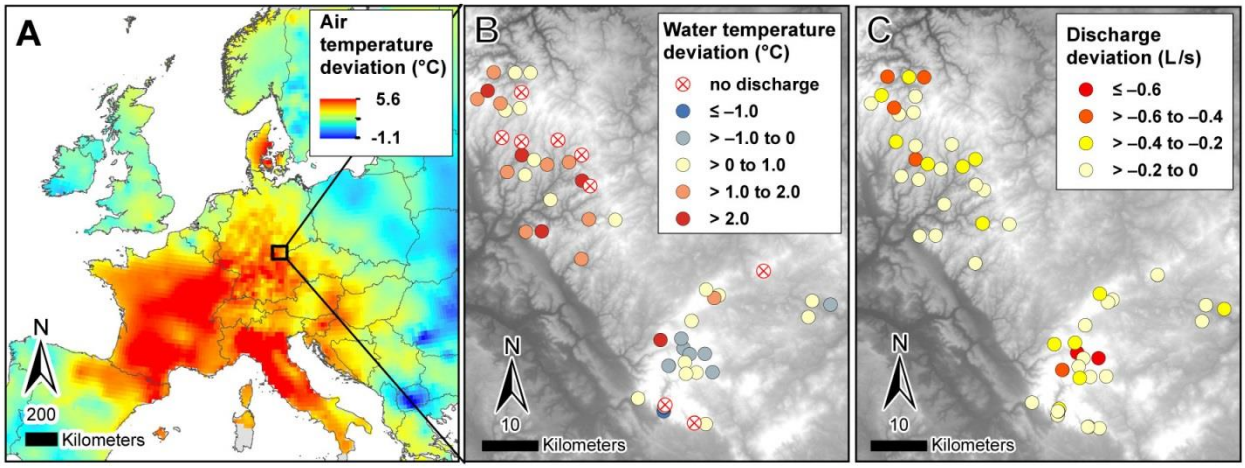

Fig. 1. Location of the studied soft water springs in Central Europe. (A) Map of Central Europe depicting the deviation of the bimonthly mean air temperature for July/August 2003 from the long-term bimonthly mean for July August (1950–2013, data source: ENSEMBLES Observations gridded dataset (E-OBS), Haylock et al. 2008). Deviation of water temperature (B) and discharge (C) of the studied springs in September 2003 from the September water temperatures/discharge rates averaged for the whole study period (1996–2006).

Data collection

We investigated spring plant community composition and hydrochemistry before (1996), during (2003) and in the three consecutive years (2004–2006) after the extreme summer of 2003. Hydrochemical data were collected in September of each year at the uppermost point of the seepage area with visible water movement to avoid any kind of short-term distorting effects caused by water-atmosphere interactions. We conducted measurements of water temperature, electrical conductivity and pH by using a portable pH-conductivity multimeter (WTW Wissenschaftlich-Technische Werkstaetten GmbH, Weilheim, Germany). Furthermore we visually estimated the water discharge rate based on a seven point ordinal scale reaching from 0 L/s up to >1.5 L/s. To quantify the buffering capacity against acidification we measured acid neutralizing capacity (ANC) ex-situ by titration (0.01 m HCL to pH = 4.3). Water sampling was not possible for nine springs in 2003, two springs in 2004 and one spring in 2005 and 2006 because of insufficient discharge (see Fig. 1B for 2003).

Vegetation was surveyed once per year between July and August. Therefore we recorded presence/absence of all vascular plant species, mosses and liverworts for each spring along a permanently

marked line-transect with a 10 cm resolution (see also Kapfer et al. 2012). Transects, which vary between 1.1 m and 24.7 m in length, span the full seepage area perpendicular to the direction of main discharge at the largest width of the well-differentiated spring site. Plants, which grew on microsites like rocks or dead wood and, thus, had no contact to the water saturated ground, were excluded from the analyses. To eliminate the bias in between site comparisons caused by differing transect lengths, species abundance along transect was standardized by dividing the number of line sections with species presence by the total number of line sections examined for the particular spring.

Data analyses

We analyzed whole community response by using a Principal Component Analysis (PCA) based on the recorded abundances of all species co-occurring along the transects of the investigated springs (vegan R package, v. 2.0-10; Oksanen et al. 2013). We quantified the extent of plant community response by calculating the Euclidean distances of each spring site in the multi-dimensional ordination space between the investigated years as well as the cumulative distance for all investigated years. Species and environmental parameters which significantly characterize the investigated springs were selected post-hoc by fitting the respective parameters on the ordination with a goodness-of-fit threshold of $r2 > 0.4$ (*envfit*()-command with 1000 permutations). We used k-means clustering to differentiate response groups of plant communities in the multi-dimensional ordination space (*kmeans*()-command based on a maximum of 1000 iterations).

For each of the selected, characteristic species we quantified the pairwise interspecific overlap of occupied environmental space with all other characteristic species before, during and after the climatic extreme event of 2003. To quantify the occupied environmental space for each of the selected species we conducted kernel-density estimations based on the five environmental parameters characterizing the spring sites where the particular species occurred: water temperature, pH, electrical conductivity, ANC and discharge (hypervolume-package for R, v. 0.9.9.7, Blonder 2014).

We tested statistical differences between our variables of interest by using the non-parametric Mann-Whitney (U) test for non-paired samples and the Wilcox (W) test for paired samples. Potential relatedness between the variables of interest was tested by using Pearson correlation. We conducted all analyses with the software environment R (version 3.0.2, R Development Core Team 2013) with a level of significance of alpha = 0.05.

RESULTS

Effects on environmental conditions

Mean discharge in 2003 of 0.14 L/s ± 0.2 L/s (arithmetic mean ± SD) was clearly lower compared to the long-term mean discharge of 0.34 L/s ± 0.28 L/s calculated for the whole study period (1996 to 2006,

Mann-Whitney U = 551, n = 57 springs, P < 0.001). Water temperature was higher in 2003 compared to the long-term mean (9.18°C ± 1.98°C compared to 8.58°C ± 1.28°C, U = 1613.5, P = 0.12). Deviations from long-term average conditions were also found for pH (5.9 ± 0.8 compared to 5.6 ± 0.6, U = 1596, P = 0.14), acid neutralizing capacity (ANC: 0.27 mmol/L ± 0.30 mmol/L compared to 0.19 mmol/L ± 0.22 mmol/L, U = 1589, P = 0.15) and electrical conductivity (112.4 µS/cm ± 107.14 µS/cm compared to 133.3 µS/cm ± 137.4 µS/cm, U = 1201, P = 0.28) although differences were not significant.

We observed a significant negative correlation between the deviation of water temperature in 2003 compared to the long-term mean and the elevation of the studied springs (Pearson r = -0.31, df = 55, P = 0.02). In other words, the lowland springs tended to be warmer in 2003, thus, strongly affected by the heat wave, whereas the upland springs tended to be less warmed up during 2003 (see also Fig. 1B). Deviation in pH during 2003 compared to the interannual mean was significantly decreased with increasing elevation (r = -0.32, P = 0.02). We observed no such correlation between deviation in discharge and elevation, which means that the effect of drought was similar for lowland and upland springs (r = -0.14, P = 0.3; Fig. 1C).

Plant community response

Principal Component Analysis (PCA) combined with the k-means clustering demarcated three groups of spring plant communities which can be seen as a result of impairment caused by previous acidification. Cumulative explanatory power of the first three axes of the principal component analyses was 38.6% of total variation. The first ordination axis, which explained 19.3% of total variation, was mainly correlated with pH and ANC. Both parameters are closely related to the acidity regime and separate neutral lowland springs form anthropogenically acidified lowland springs. The second axis, which explained 10.1% of total variation, was mainly correlated with elevation and water temperature and delimited cool, naturally acid highland springs from the springs of lower elevations.

The community groups, named in the following: neutral lowland springs, acidified lowland springs and upland springs, showed significant differences in the response to the extreme climatic event of 2003 in terms of species assemblage and characteristic species (Fig. 2A). Species which significantly characterize the three community groups are *Chrysosplenium oppositifolium* L., *Impatiens noli-tangere* L. and *Brachythecium rivulare* Schimp. for the neutral lowland springs as well as *Sphagnum fallax* (H. Klinggr.) H. Klinggr. and *S. palustre* L. for the recently acidified lowland springs. *Calamagrostis villosa* (Chaix) J.F.Gmel. characterizes the upland springs. We observed a high resilience of neutral lowland springs to the climatic extreme event of 2003 (expressed by relatively small point size and shifts of convex hulls in Fig. 2A and B, respectively). In contrast, we observed strong initial response, thus, low resilience for the acidified lowland springs. For the upland spring communities, we found the strongest response in 2003, thus, lowest resilience among all three community groups. Community composition of these upland springs shifted towards the acidified lowland springs. However, the highland communities showed high elasticity by returning to the initial pre-2003 state right after the extreme in 2004 and overall shift in community composition was lower than for the acidified lowland springs.

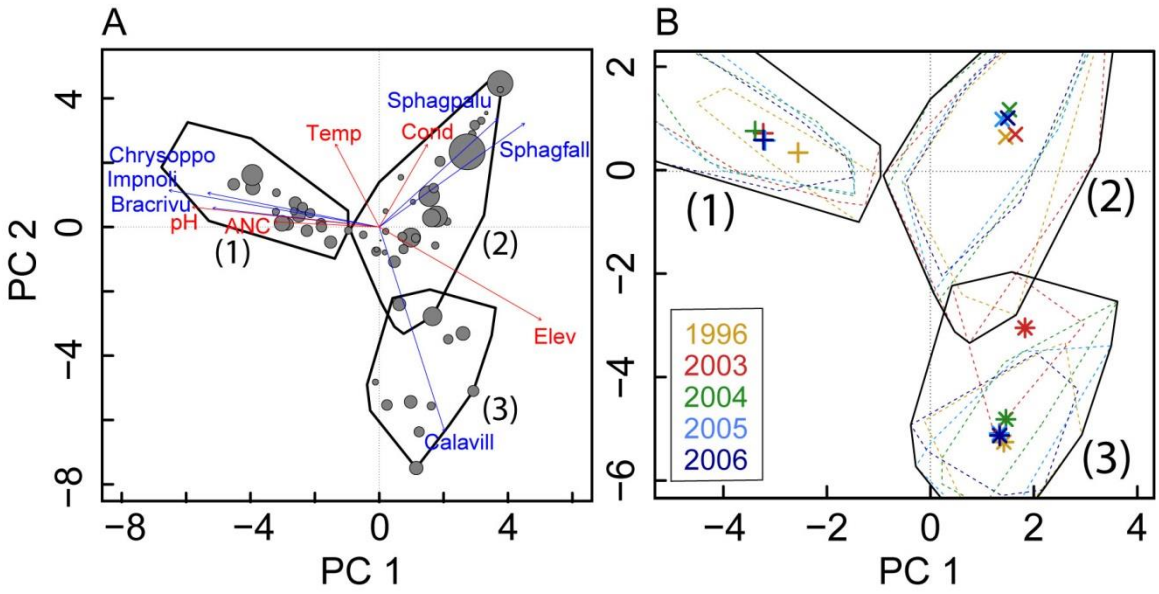

Fig. 2. Short-term vegetation response of springs in community composition to the climatic extreme summer 2003 (results of a Principal Component Analysis). (A) The three different community groups (black hulls, 1: neutral lowland springs, 2: acidified lowland springs and 3: upland springs) are mainly differentiated by temperature (Temp: water temperature and Elev: elevation) as well as by the acidity regime (pH, and ANC: acid neutralizing capacity) reflected in different character species (blue arrows). (B) Temporal shifts in species composition within the three community groups. Depicted are group centroids (plus signs: neutral lowland springs, crosses: acidified lowland springs and asterisks: upland springs) and outer margins (dashed lines in different colours) for the particular years. Size of grey points (A) depicts the extent of initial community reaction (2003–2004) in the particular springs. Abbreviations are Chrysoppo: *Chrysosplenium oppositifolium*, Impnoli: *Impatiens noli-tangere*, Bracrivu: *Brachythecium rivulare*, Sphagfall: *Sphagnum fallax*, Sphagpalu: *Sphagnum palustre*, Calavill: *Calamagrostis villosa* and Cond: electrical conductivity.

Single species response

For the characteristic species of the three community groups demarcated by the PCA we observed a strong but not uniform change in the volume of occupied environmental space during the extreme summer of 2003 (Fig. 3). The strongest increase in occupied environmental space was found for the moss *Brachythecium rivulare*, followed by the moss *Sphagnum fallax* and the annual herb *Impatiens noli-tangere*. The perennial clonal herb *Chrysosplenium oppositifolium* showed a slight increase during 2003. In contrast, we observed losses in occupied environmental space for the moss *Sphagnum palustre* and the perennial clonal grass *Calamagrostis villosa*.

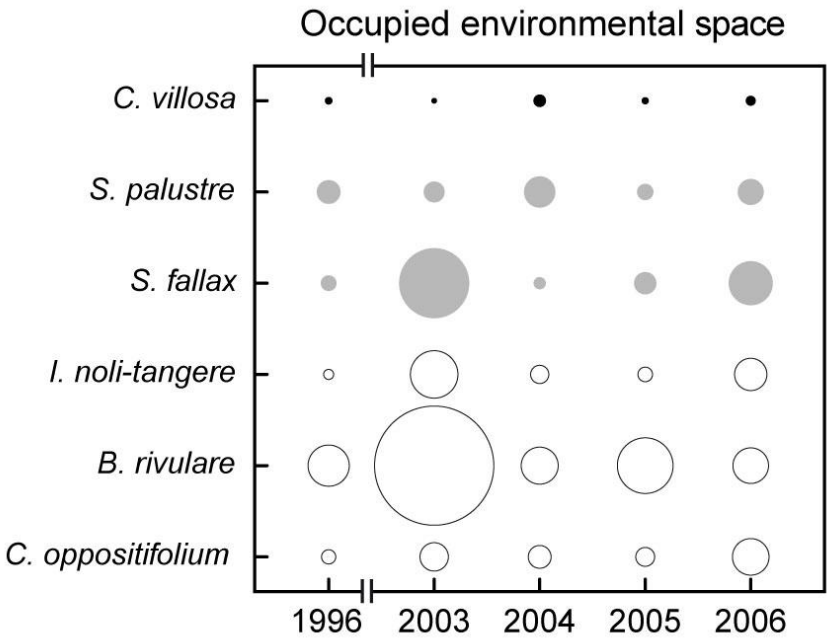

Fig. 3. Temporal variation in occupied environmental space for the plant species characterizing soft water springs in Central Germany. Point size depicts the volume of occupied environmental space in the particular year (based on the n-dimensional hypervolume for the particular species). The different colors depict the community groups which are characterized by the different species (white: neutral lowland springs, grey: acidified lowland springs, black: upland springs).

Temporal variation in occupied environmental space (coefficient of variation [cv]) was highest for *Sphagnum fallax* (cv = 0.74) followed by *Impatiens noli-tangere* and *Brachythecium rivulare* (cv = 0.62 and 0.61, respectively). Lowest temporal variation was observed for *Sphagnum palustre* (cv = 0.24), while *Chrysosplenium oppositifolium* and *Calamagrostis villosa* performed intermediate temporal variation in occupied environmental space (cv = 0.36 and 0.32, respectively).

Significant impacts of the climatic extreme summer of 2003 on the interspecific overlap of occupied environmental space were detected (Fig. 4). We observed a decrease in the overlap between *Calamagrostis villosa*, which characterizes upland springs, and all other lowland spring species from 32% in 1996 to 16% in 2003 (mean difference 16%, W = 15, P = 0.06). In contrast, overlap between *Sphagnum fallax* and common species such as *Chrysosplenium oppositifolium*, *Brachythecium rivulare* and *Impatiens noli-tangere* increased in 2003 on average from 18% to 37% (mean difference 19%, P = 0.25).

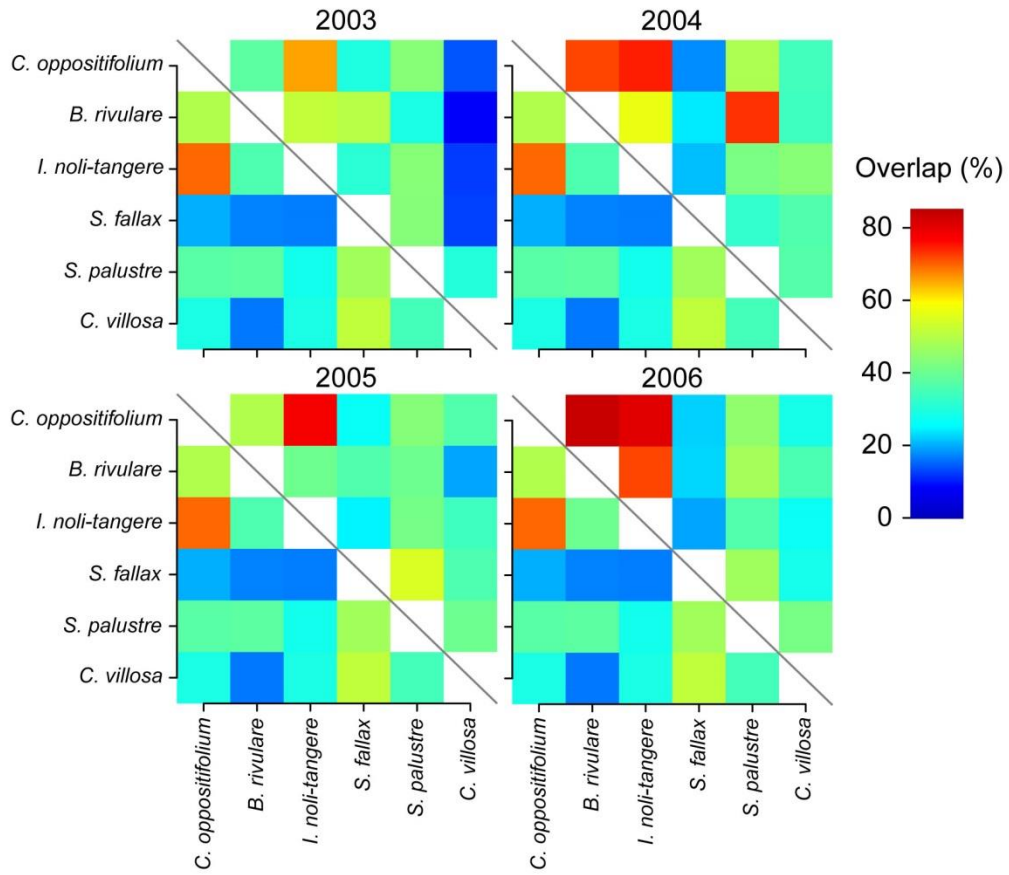

Fig. 4. Temporal variation of overlap in occupied environmental space (2003–2006) between species characterizing neutral lowland springs (*C. oppositifolium*, *B. rivulare*, *I. noli-tangere*), acidified lowland springs (*S. fallax*, *S. palustre*) and upland springs (*C. villosa*). Overlap of the particular year is depicted in the upper right half of each plot, whereas pre-2003 niche overlap (1996) is shown as reference in the lower left half of each plot.

DISCUSSION

Biotic responses to climatic extreme events are extensively studied for experimentally controlled, artificial ecosystems on spatially restricted, local scale (Smith 2011 and references therein, Jaeschke et al. 2014). Knowledge is scarce when it comes to uncontrolled, natural ecosystems on larger spatial scales (Easterling et al. 2000, Smith 2011). Here we show for an uncontrolled ecosystem on landscape-scale that biotic response of plant communities to the extreme conditions of the year 2003 is clearly related to the systems' history in terms of anthropogenic acidification. This was found for single species as well as for species assemblages and plant communities.

Extensive and prolonged summer drought has been reported for freshwater systems to significantly interact with acidification (Schindler et al. 1996, Schindler 1997). Here, we show that spring communities previously impaired by anthropogenic acidification clearly differ in terms of ecological resilience and elasticity compared to springs previously less affected by acidification. We observed high community

resilience for neutral lowland springs unaffected by historic pollution but low resilience for lowland springs that were exposed to acidification. In other words, pristine lowland springs which were previously not strongly affected by acidification were significantly more resilient, thus, more prone to prolonged summer droughts than springs which are already destabilized by acid rain. Upland springs which were affected in discharge (drought) similar to lowland springs but were significantly less affected in water temperature (heat wave) showed lower resilience but higher elasticity than lowland springs.

In contrast to anthropogenic atmospheric acidification, natural acidification is a consequence of long-term processes that require time spans such as millennia. Podzolic traits in upper soils are formed under high precipitation combined with low temperature and subsequently low carbon turnover. Spring communities that are located in catchments with these properties had enough time to adapt to the naturally acidic conditions. Comprehensibly, upland springs which are characterized by naturally acid conditions showed lowest resilience but high elasticity to the climatically extreme summer of 2003. The strong initial reaction of the upland spring community is linked to water temperature as the direction of the water temperature effect in the ordination follows the same direction as the shift of this community.

Extreme climatic events will affect the performance of individual species in different ways and, thus, alter community composition (Parmesan and Yohe 2003, Thibault and Brown 2008). However, communities exposed to fluctuating environmental conditions are more prone to abrupt climatic changes than communities adapted to environmental stability (Walther et al. 2002). Spring plant communities are commonly expected to consist of very specialized taxa that are evolutionary confined to stable environmental conditions and, thus, should reveal low ecological resilience and elasticity in face of extreme climatic events. Although we observed the community response to the extreme climatic event to be dependent on acidification history, we observed surprisingly high elasticity of single species populations and whole spring plant communities to the climatic extreme summer of 2003.

Biotic compensation against the climatic extreme summer 2003 on community level results from the variance in response characteristics of single plant species. Species-specific responses within the neutral lowland spring community were characterized by high heterogeneity in the extent of reaction. Both, the moss *Brachythecium rivulare* and the annual herb *Impatiens noli-tangere* performed high elasticity but low resilience, whereas high resilience was observed for the perennial and clonal herb *Chrysosplenium oppositifolium*. Similar patterns were found for the acidified lowland springs, where *Sphagnum fallax* showed higher response flexibility compared to *S. palustre*. This is in accordance with the conceptual idea of the insurance hypothesis, which states that asynchronous responses of different species contribute to overall community stability against environmental fluctuations (Folke et al. 1996, Naeem and Li 1997, Yachi and Loreau 1999).

Chrysosplenium oppositifolium is known from several studies to be closely associated to neutral lowland springs in mountain ranges of Central Germany. In these lower elevations, *Sphagnum fallax* indicates anthropogenic acidification (Audorff et al. 1999). Furthermore, *Sphagnum fallax* is known to be significantly promoted by nutrient input (Twenhoeven 1992) and can be classified as a competitive species which profits from the consequences of acidification and nutrient deposition (Limpens et al. 2003). In addition, this species which is rather tolerant to desiccation (Sagot and Rochefort 1996) and is

able to actively enhance local acidification in its habitat through cation exchange processes (Soudzilovskaia et al. 2010). All these characteristics enable *Sphagnum fallax* not only to temporally invade neutral lowland springs during prolonged drought periods but also permanently shift these systems towards novel ecological states. According to that, the significant increase in the interspecific overlap of occupied environmental space we observed for all of the characteristic species of neutral lowland springs with *S. fallax* indicates that this competitive moss is increasingly interacting with these species in times of environmental changes (and stress). This increase in the interspecific overlap for the species of neutral and acidified lowland springs, which occurred after 2003, supports evidence for invasion processes.

CONCLUSIONS

An increasing frequency of severe droughts, which is expected for the near future (IPCC 2014), is very likely to weaken pristine spring plant communities and stimulate the immigration of species. Such enhanced establishment of new species will lead either to homogenization of communities or trigger community shifts into alternative stable states.

As frequency and intensity of drought periods and heat waves will significantly increase during the next decades, interactions between abiotic and biotic non-linear dynamic processes and historical legacies leading to tipping points and subsequent alternative states are likely to become important in many ecosystems. However, the threat to local biodiversity is especially high in less disturbed and isolated plant communities such as springs.

The environmental parameters measured in this study seem to be all those necessary to sustain the argumentation of our study. However, future studies about the interaction of abiotic and biotic elements in these ecosystems should also elaborate on other environmental factors like nutrient availability and toxic elements to fully understand community responses to abrupt climatic shifts.

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5.3 Manuscript 3

Salt in the wound: The interfering effect of road salt on acidified forest catchments

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Highlights

- Road salt significantly affects acidity regime of road adjacent forest catchments.
- Peak water concentrations of Na and Cl occurred during snowmelt periods (April/May).
- Water concentrations of Na and Cl remained constantly high throughout the whole year.
- Road salt seems to increase the leaching of soil cation nutrients (K, Mg and Ca).
- Effects were detectible up to a distance of 830 m from the road.

Abstract

Atmospheric acidic depositions have strongly altered the functioning and biodiversity of Central European forest ecosystems. Most impacts occurred until the end of the 20th century but the situation substantially improved thereafter caused by legal regulations in the late 1980's to reduce acidifying atmospheric pollution. Since then slow recovery from acidification has been observed in forested catchments and adjacent waters. However, trends of recovery are inconsistent and underlying mechanisms diminishing recovery are still poorly understood.

We propose that the input of road salt can significantly affect acidity regime and acidification recovery of forest ecosystems.

By comparing the discharge hydro-chemistry and plant community composition of springs fed by forested catchments with and without high levels of salt input over two decades we observed a significant suppression of recovery and elevated levels of nutrient leaching (K^+, Ca^{2+} and Mg^{2+}) in highly salt contaminated catchments. We show that the pollution of near-surface groundwater (interflow) by road salt application can have lasting effects on ecosystem processes over distances of several hundred metres apart from the salt emitting road.

Keywords

atmospheric pollution; catchment biogeochemistry; nutrient leaching; snow and ice control; sodium chloride; thawing salt

1. Introduction

During the second half of the 20th century, the emission of sulphuric and nitrogenous gases which peaked in the late 1980's resulted in large-scale acidification of forest soil and groundwater. Even remote forests and aquatic ecosystems were harmed in large parts of Europe and North America (Almer et al., 1974; Wright, 1983; Reuss et al., 1987; Matzner and Murach, 1995). The large-scale deposition of acidifying pollutants strongly changed biogeochemical processes and equilibria in terrestrial and aquatic ecosystems (Rice and Herman, 2012). Sulfur and nitrogen oxides (SO_4^{2-} and NO_3^-) originating from airborne pollution caused the displacement of acidifying and toxic elements (H^+ and Al^{3+}) but also the leaching of important nutrients (K^+, Ca^{2+} and Mg^{2+}) from soils with detrimental ecological effects on forest and the subsequent freshwater ecosystems. Since then atmospheric deposition of acidifying pollutants decreased significantly as a consequence of the implementation of technology that is more efficient and emits less pollutants (Nyiri et al., 2009; Pihl Karlsson et al., 2011). However, forest and adjacent freshwater ecosystems are slowly recovering from this long-lasting impact (Hruška et al., 2002; Holmberg et al., 2013). Furthermore, patterns of recovery differ remarkably between sites (Pihl Karlsson et al., 2011) probably related to specific environmental settings.

Recovery processes were shown to depend on various environmental factors like the distance to the former source of acidic emission (Pihl Karlsson et al., 2011), which is probably related to critical loads, as well as on climate, soil, bedrock composition, and other environmental factors unrelated to anthropogenic acidification (Wright and Jenkins, 2001; Skjelkvåle et al., 2003). However, the full extent of environmental drivers which enhance or delay recovery processes is not sufficiently understood and major pieces are missing to resolve the puzzle of ecosystem recovery after acidification. Thus, human induced acidification is still a serious footprint of environmental pollution (Larssen and Holme, 2006).

Besides other environmental factors which are able to interfere with recovery, numerous studies from Scandinavia hint at a significant influence of sea salt deposition causing short-term acidification peaks that hinder long-term recovery of forested ecosystems from anthropogenic acidification (Hindar et al., 1995; Wright and Jenkins, 2001; Larssen and Holme, 2006; Skjelkvåle et al., 2007; Laudon, 2008; Akselsson et al., 2013). This so called ‘sea salt effect’ (Wiklander, 1975) is caused by cation exchange processes induced by an excessive input of sodium (Na^+). While sodium is retained in the soil, H^+ ions are exchanged which inevitably supports acidification of soil- and surface-waters.

Since the 1960's, road salt is the main de-icing agent in Europe and North America during winter (Green et al., 2007). Usually the most cost-efficient and widely used de-icing agent is sodium chloride (NaCl, c.f. BayLfW, 1999; Green and Cresser, 2008). This widespread form of road salt is similar to sea salt in its chemical structure and ecological behaviour. The negative environmental effects of road salt application were perceivable since the very beginning of its application (Judd, 1969). However, most studies focused on short-term effects on particular organisms or habitats directly adjacent to the salted roads. Although there are some studies which focused on long-term trends of road salt in streams and groundwater not directly adjacent but still affected by road salt application (e.g., Godwin et al., 2003; Findlay and Kelly, 2011), there is a current lack of knowledge about its effects on distant forest areas that come in contact with salty groundwater. However, the topic of large-scale ecological effects of road salt

application is of growing importance as road salt application continuously increased during the last decades.

The high density of roads and increasing traffic has caused high levels of road salt application during the last decades. To keep traffic flowing, between 0.61 and 3.5 million tons of road salt (1.6 million tons on average) was applied annually during winter on Germany's highways be- tween 1992 and 2005 depending on weather conditions (Statista, 2015). Astebol et al. (1996) report 75% to 90% of applied sodium chloride to enter the road-adjacent environment by deposition and/or melting of contaminated snow. Several studies report a significant input of road salt in distant areas especially during spring-time via surface and sub-surface run-off or via groundwater (BayLfW, 1999; Blasius and Merritt, 2002 and references therein). However, little knowledge exists about the effects of road salt application on the recovery rates of acidified forest ecosystems, although the ecological effects caused by road salt (NaCl) have to be assumed to be similar to the effects reported for sea salt deposition.

The ecosystems investigated in this study were heavily impacted by the deposition of acidifying pollutants (SO_4^{2-} and SO_2^{-}) during the 1970s to early 1990s which resulted in strong acidification of the forest and subsequent springs and riverine ecosystems in this region (Matzner and Murach, 1995). Since then the ecological effects of former acidification are slowly decreasing but are still detectable in the chemical properties and plant community composition of the spring /forest ecosystems under study (Alewell et al., 2000; Schweiger and Beierkuhnlein, 2014). The investigated springs are mainly fed by surface-near groundwater originating from predominantly forested catchments. By percolating through the soil layers of the catchments the water takes up soluble compounds originating from the whole catchment. At the spring site the upwelling groundwater with its solutes then reflects the geochemical traits of the catchments. Plants which inhabit these springs strongly rely on the prevalent environmental conditions (temperature, hydrochemistry) which are known to be very stable under pristine conditions (Strohbach et al., 2009; Audorff et al., 2011; Schweiger and Beierkuhnlein, 2014). Such specialized and highly adapted species react very sensitively to hydro-chemical changes of the spring water and, thus, shifts in biogeochemical processes in their catchments. In consequence, monitoring of spring hydro-chemistry and plant community structure allows for a spatially as well as temporally integrative assessment of biogeochemical processes of the forested catchments. When repeated multiple times in small catchments, long-term biogeochemical processes can even be assessed at the landscape scale in the absence of other acidifying processes such as forest clearing.

In this study we used springs as a (bio-) monitoring tool to assess how road salt application contributes to the behaviour of acidified forested catchments. In addition to repeated measurements of abiotic conditions we used plant indicator values of Ellenberg et al. (2001) as a biomonitoring tool to quantify environmental conditions indicated by the species' occurrence. Based a multitude of field studies for all Central European plant species (including ferns, horsetails, mosses and liverworts) indicator values for their ecological behaviour regarding major site conditions are defined. One category of indicator values concerns species response to acidity regimes (R-value), which are important for nutrient solubility and thus availability but also for the solubility of toxic compounds. The availability of such values for all plant species is an extraordinary advantage in European vegetation science. This explains why this method

is actually widely applied in environmental impact studies (e.g., Koch and Jurasinski, 2015; Kuechler et al., 2015).

We monitored water chemistry and plant community composition of 52 springs in the lower mountain ranges of Central Germany over a period of 25 years (1989 to 2014). All investigated springs are characterised by a constantly water saturated, thus, swampy (seepage) area in which the investigated plant communities have established. Resulting from the spatially diffuse emergence of groundwater, the investigated spring sites have a spatial extent of a few to several hundred square metres (Schweiger and Beierkuhnlein, 2014). Whereas most of these springs are more than 1000 m apart from main roads or in higher elevation, four of these springs are located between 150 and 830 m downslope of a road where salt is frequently applied during wintertime. In consequence, the discharge of these springs exhibits very high concentrations of sodium chloride in comparison with the control group of springs (n = 48). This situation provided an opportunity to study the effects of road salt on forested catchments.

Similar to the historic acidification caused by airborne pollutants, the major compound of de-icing agents, sodium (Na^+) is not only reported to cause the release of acidifying elements (H^+) but also to increase the leaching of important nutrients (K^+, Ca^{2+} and Mg^{2+}). Continuous road salt application might, thus, continue the biogeochemical and subsequent ecological effects of historic acidification and, therefore impair the long-term recovery of forested and subsequent freshwater ecosystems. Though the term ‘recovery’ is ambiguous and not very precise we are using it in this study as follows: recovery does not mean total or complete restoration of a former state. First, such states have also been under transition, but very likely in different time scales and speed. Defining a precise reference state is difficult because the chosen reference time is arbitrary. Second, today's conditions will certainly differ not only according to one target variable (e.g., acidity) but also in other respect (e.g., climate). And third, we are not interested in a certain status but in processes that are going on. This is why we understand ‘recovery’ as a term that indicates the direction of detected trends, away from unfavourable states such as high acidity, high loads of heavy metals, or imbalanced nutrient availability. Like this it is feasible to talk about ‘recovery’.

Depending on the distance to the sources of application (roads) as well as on the predominant vegetation and land use, we assume the catchments and their springs to be differently affected by road salt contamination and the concomitant biogeochemical processes. We hypothesise that (1) similar to the ‘sea salt effect’ (Wiklander, 1975) road salt application significantly affects the acidity regime of forested catchments and impairs long-term recovery from former anthropogenic acidification. We furthermore hypothesise that (2) the strength of this ‘road salt effect’ decreases with increasing distance to the road.

2. Materials and methods

The monitored spring sites are located in the lower mountain ranges of Central Germany (Frankenwald, 50° 11′ to 50° 31′ N, 11° 15′ to 11° 40′ E). The sites were selected by considering comparable pedo- and geogenic conditions, forest composition and morphological site characteristics (see Table 1).

Table 1. Characteristics of the springs and the associated forested catchments in the lower mountain range of Central Germany. Values are depicted separately for the four road salt impacted springs and are summarized for the salt impacted springs and all other springs (mean and standard deviation, other springs n = 48). Values for discharge are based on water sampling conducted in September of each investigated year between 1989 and 2013 (n = 6 years). Seepage area quantifies the water saturated area of the spring sites. Positive elevational differences to the nearest road stand for springs lying above the nearest road, negative values for springs below the nearest road. Besides the predominant soil texture in the catchments, forested as well as agricultural areas are depicted in percent of the total catchment area.

Spring	Distance to next road [m]	Elevational difference to next road [m]	Seepage area [m²]	Discharge [L s^{-1}]	Forested area [%]	Agricultural area [%]	Soil texture
1	154	-18.5	115	0.40 ± 0.20	60	11	Clay/sand
2	205	-47.2	33	0.03 ± 0.02	88	0	Clay
3	348	-10.5	69	0.60 ± 0.50	87	0	Clay
4	830	-79.3	83	0.30 ± 0.20	71	6	Sand
Average (1-4)	384 ± 308	-38.9 ± 31.2	75 ± 34	0.22 ± 0.20	77 ± 13	4 ± 5	
All other springs	1287 ± 722	55.3 ± 116.3	103 ± 120	0.30 ± 0.30	78 ± 30	10 ± 20	Clay

The four salt impacted spring sites are located downslope of a main road which runs along a mountain ridge (see Fig. 1c). As the application of road salt as well as snow clearing and traffic loads occur in the same intensity and frequency along this main road, the initial settings can be assumed to be similar for all four springs.

Furthermore, the investigated springs are located very close to the former inner German border as well as to the Czech Republic (see Fig. 1a). This means high loads of acidifying pollutants originating from combustion heavily impacted the forested catchments in these regions during the 1970s and 1980s (Alewell et al., 2000). Since the fall of the former inner German border in 1989 and the coincident policy-related decrease of acidifying emissions, water chemistry and spring plant community composition of 52 springs in total were frequently investigated during a period of 25 years (1989 to 2014) to monitor the processes and patterns of forest and spring recovery, including the four springs which are of interest in this study.

The springs, which are defined as helocrenic (seepage) spring type according to Thienemann (1924) are characterised by a spatially rather diffuse emergence of slow flowing water (mean discharge = 0.3 L/s) resulting in a water saturated (seepage) area of 75 ± 34 m^2 on average (mean and standard deviation, n = 4 springs, see Table 1). The forested catchment areas of the four springs along the road as well as the 48 other springs in the study area are dominated by Norway spruce (*Picea abies* (L.) H. Karst.) with a low intermixture of European beech (*Fagus sylvatica* L.). The dense bedrock of the study area predominantly consists of schist, which prevents precipitation from penetrating in deeper layers and most of the percolated soil water is transported as interflow in conductive near-surface layers (Kleber et al., 1998). Therefore, hydro-chemical spring water characteristics are expected to be closely linked to biogeochemical processes in the forested catchments (Beierkuhnlein and Durka, 1993; Strohbach et al., 2009).

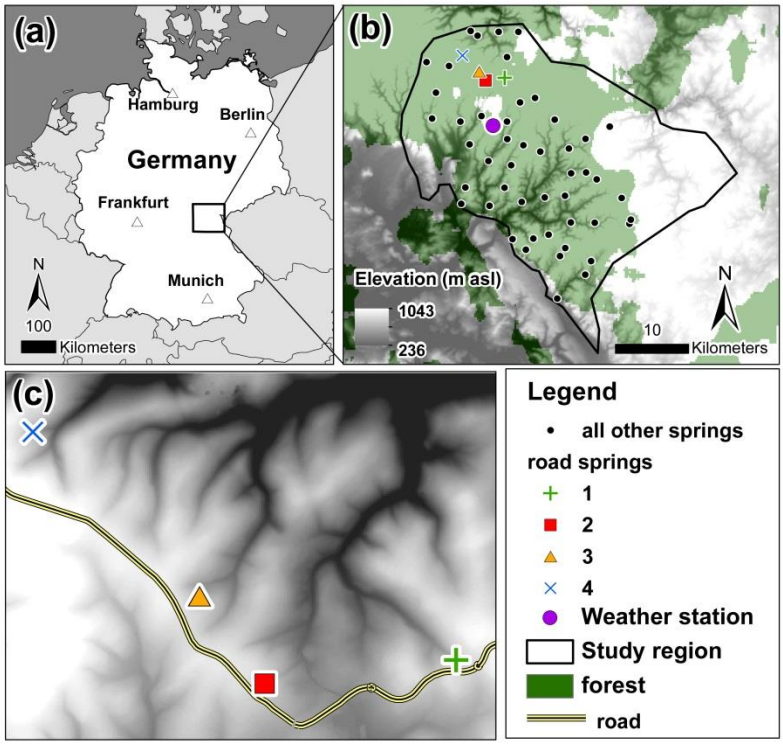

Fig. 1. Location of the road salt impacted springs in Central Germany. a) Overview, b) location of the four road salt impacted springs (coloured symbols) and all other springs investigated in the study area as well as the weather station (in Teuschnitz) used to obtain snow cover data, c) Detailed location of the road salt impacted springs in different distances offstream a state road with frequent road salt application during winter months.

Hydro-chemistry of spring water was sampled in late September and October of each investigation period. Acidity regime (pH) and plant community composition were investigated at six occasions between 1989 and 2013 (1989, 1996, 2003, 2004, 2005 and 2013). The hydro-chemical concentrations of important nutrient elements were quantified at four occasions during 1996 to 2013 (1996, 2003, 2004 and 2013). Analyses focused on compounds that are known to be significantly affected by acidification (Mg^{2+}, Ca^{2+} and K^{+}, Singh and Agrawal, 2008). In addition road salt related elements (Na^{+} and Cl^{-}) were measured. During two periods, we monitored the seasonal variation of water chemistry for two full-year courses. This was carried out in 2003/ 2004 (from September to September) and 2013/2014 (from May to May) with monthly water sampling (equals 12 samples for all 52 springs for each annual course).

We measured pH on-site by using a portable pH-conductivity multimeter with a liquid electrolyte pH-probe and a conductivity probe (WTW pH/Cond 340i with WTW SenTix 81 and WTW TetraCon 325, Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany). Water sampling was conducted at the uppermost point of the seepage area with visible above-ground flow to avoid potential distorting effects on water pH or chemistry. Besides the degassing of CO_2, which can strongly affect water pH instantly after the ground water appears at the surface, biotic effects caused by the spring inhabiting plant species can for instance modify water chemistry. Concentrations of dissolved elements related to road-salt

input (Cl^-, Na^+) were analysed ex-situ from filtered water samples (0.45 µm cellulose acetate filters, Satorius Stedim Biotech GmbH, Goettingen, Germany). The same was true for important nutrient elements (K^+, Ca^{2+}, Mg^{2+} and NO_3^-) which were previously shown to be impacted by cation exchange processes induced by salt (NaCl) contamination (Wiklander, 1975; Green and Cresser, 2008). Water concentrations of Cl^- and NO_3^- were analysed by using ion chromatography (881 Compact IC Pro, Metrohm) whereas concentrations of Na^+, K^+, Ca^{2+} and Mg^{2+} were quantified with an ICP-OES (Inductively Coupled Plasma-Optical Emission Spectroscopy, Vista – Pro, Autosampler ASX-510, Varian Inc./Cetac).

To investigate long-term variation of spring plant community composition we determined all vascular plants growing in the water-saturated seepage area of the springs during July and August in 1989, 1996, 2003, 2004, 2005 and 2013. We quantified the abundance of all occurring species with cover estimates based on a modified Braun–Blanquet approach (for further details see Schweiger and Beierkuhnlein, 2014). In addition to the pH measurements of spring water, we concluded on the acidity regime indicated by plant community composition by using species-specific Ellenberg indicator values for acidity for all recorded species. Ellenberg indicator values quantify for a particular plant species the position of its realized niche along a certain environmental gradient (i.e., acidity). In other words, the index values for acidity range from 1 (species indicating very acid conditions) to 9 (species indicating alkaline conditions) and, thus, characterise the acidity regime of a particular site where the particular species occurs in competition with other species (Ellenberg et al., 2001). In our study we used plant species' abundances quantified for each spring and year during the vegetation records to weigh the Ellenberg indicator value of acidity for each detected species. Subsequently, we calculated a community weighted mean of the indicator value for all years and for each spring to retrieve spatial and temporal information on community-indicated acidity regimes.

We tested temporal trends of pH and community indicated acidity regime using Pearson correlation and linear regression models by considering the statistical requirements of the test/model. Analyses of long-term trends and differences in the abiotic conditions are based on water sampling conducted in September of each investigated year between 1989 and 2013 (for pH) and 1996 to 2013 (for all other elements/compounds). Statements on short-term (annual) variation are based on the monthly water sampling conducted during 2003/04 and 2013/14. Differences in hydro-chemical parameters among the investigated springs were tested with the non-parametric Mann–Whitney-U test for non-paired samples. All analyses were conducted in the R environment (v. 3.0.2, R Core Team, 2013) with a level of significance of alpha = 0.05.

3.Results

3.1. Effects of road salt on the water chemistry and plant community composition of forest springs

Except for the spring closest to the road (spring 1), a clear spatial pattern was observable for the hydro-chemistry of the investigated springs. Concentrations of elements related to road salt input (Na^+ and Cl^-) were exceptionally high for road adjacent springs but decreased with increasing distance from the salt emitting road. Furthermore, concentrations of important nutrients (K^+, Mg^{2+} and Ca^{2+}) in the discharge of the springs were significantly elevated in road adjacent springs and decreased with increasing distance from the road. Measured pH was low in road adjacent springs and increased with increasing distance. These patterns were observed for the long-term trends (Fig. 2, Table 2) as well as the seasonal dynamics (Fig. 4) of water chemistry for the investigated springs.

We found water concentrations of sodium (Na^+) measured for the four salt impacted springs along the road to be approximately ten times higher than Na^+ concentrations of all other (48) springs in the study region (mean concentrations for the period 1996–2013: 50.3 mg L^{-1} vs. 5.8 mg L^{-1}, Mann Whitney-U = 1883.0, $p < 0.001$, Fig. 2). Mean concentrations of chloride were almost 12 times higher in the springs with salt impacted catchments compared to the other, non-affected springs (96.5 mg L^{-1} vs. 8.1 mg L^{-1}, U = 1868.5, $p < 0.001$). During the two full-year courses of monthly measurements (2003/04 and 2013/14) we observed maximum concentrations among the salt impacted springs of 251 mg L^{-1} for sodium and 426 mg L^{-1} for chloride during periods of snowmelt (April/May) in a spring 200 m (air-line distance) downstream of the road (spring 2, Figs. 1 and 4). With increasing distance of the salt impacted springs to the road, we observed a general decrease of Na^+ and Cl^- concentrations (Table 2) with maximum concentrations during snowmelt of 10.9 mg L^{-1} (Na^+) and 19.8 mg L^{-1} (Cl^-) 830 m from the road.

Along with the significantly increased concentrations of sodium and chloride we observed significantly lower pH values for the road adjacent springs compared to all other non-impacted springs (mean pH 1996-2013: 5.5 vs. 6.1, U = 910.5, $p = 0.004$). Among the salt impacted springs pH values increased with increasing distance to the road (Fig. 2c, table 2). However, the spring closest to the road (spring 1) did not follow this pattern, neither for road salt concentrations nor for measured pH. Although the spring is the closest to the road, concentrations of Na^+ and Cl^- were comparably low whereas pH was exceptionally high (spring 1, Fig. 2, Table 2). Furthermore, this spring showed significantly increased average concentrations of nitrate, which were 3.4 times higher than the concentrations of all other (51) investigated springs (NO_3^- = 21.1 mg L^{-1} vs. 6.3 mg L^{-1}, U = 548.0, $p = 0.001$).

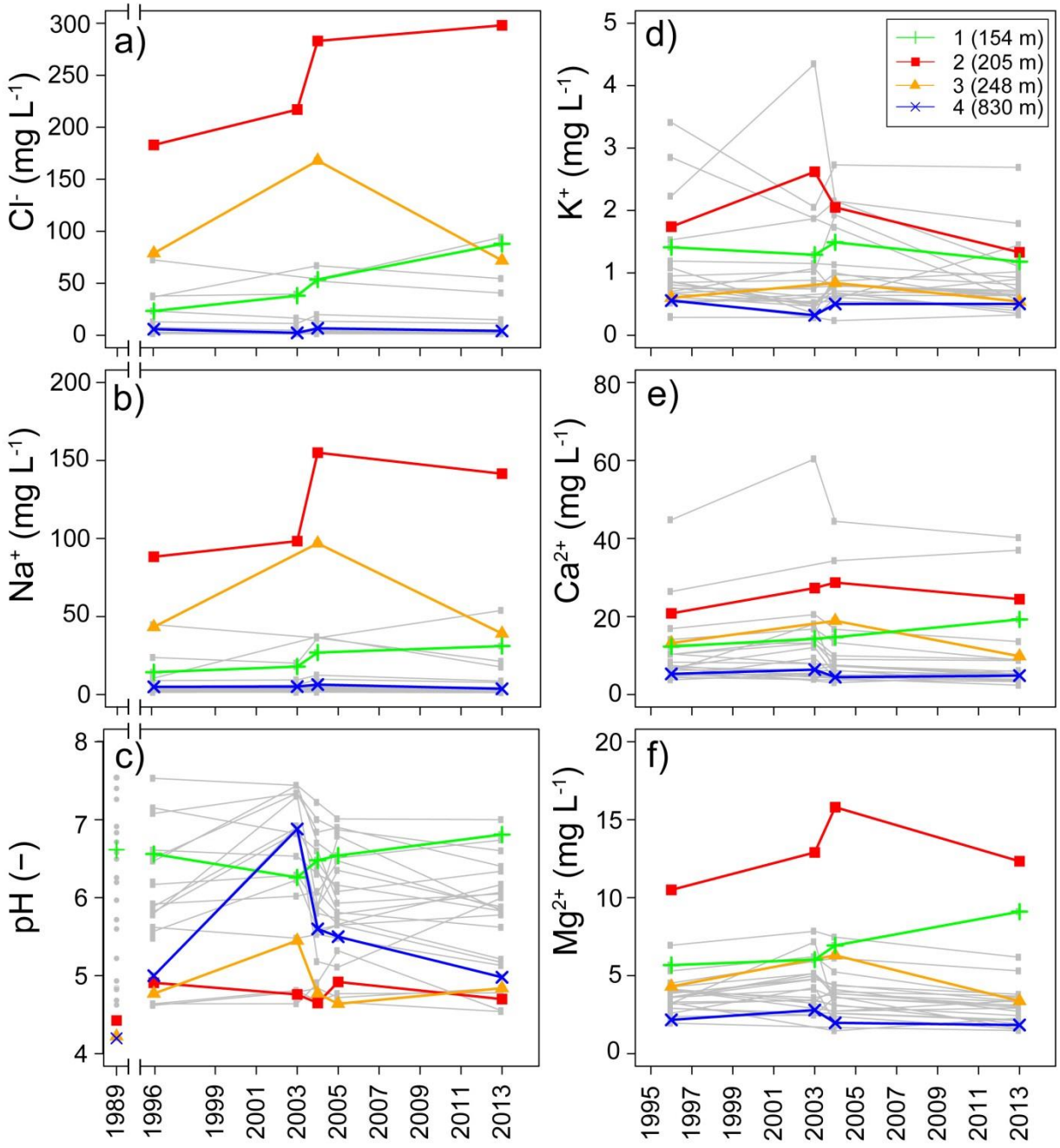

Fig. 2. Long-term trends of concentrations of road salt related cations (a and b), pH (c) and concentrations of important soil nutrients (d–f) measured during September of each monitored year in the water of forest springs lying in different distances offstream a state road with frequently road salt application during winter months. Salt-impacted springs are marked by coloured individually marked lines; non-impacted springs are depicted as grey lines (distance of the salt impacted springs to the road is depicted in parenthesis).

Table 2. Abiotic characteristics and long-term trends in acidification recovery of the monitored springs in different distances to a state road in Central Germany with frequent road salt application during winter months (individual values and summary for the four road salt impacted springs and summary for the other springs, n=48). Values of hydro-chemical parameters depict mean and maximum (in parenthesis) for individual (salt impacted) springs and mean ± standard deviation for summary based on September measurements (pH: 1989 to 2013, all other parameters: 1996-2013). Statistics of long-term trends in measured pH and acidity regime indicated by spring plant community composition (using community weighted Ellenberg indicator values) are depicted parallel. Shown are slopes and p values of ordinary least squares regression models. A positive slope indicates decreasing measured/indicated acidity (significant trends are printed in bold face).

Spring	Distance to road (m)	Cl^- (mg L^{-1})	Na^+ (mg L^{-1})	K^+ (mg L^{-1})	Mg^{2+} (mg L^{-1})	Ca^{2+} (mg L^{-1})	NO_3^- (mg L^{-1})	pH (−)	Long-term trends (1989–2013)			
									Measured pH (−)		Indicated acidity (−)	
									Slope	p-Value	Slope	p-Value
1	154	50.8 (87.9)	22.5 (31.1)	1.3 (1.5)	6.9 (9.1)	15.1 (19.3)	21.1 (23.4)	6.5	0.0049	0.66	**0.0340**	**0.047**
2	205	245.3 (298.0)	120.8 (155.0)	1.9 (2.6)	12.9 (15.8)	25.3 (28.7)	6.2 (16.8)	4.7	0.0097	0.41	0.0285	0.34
3	348	85.2 (168.0)	52.7 (96.9)	0.7 (0.8)	4.5 (6.3)	13.4 (18.9)	6.6 (9.9)	4.8	0.0250	0.30	**0.0369**	**0.033**
4	830	4.8 (6.8)	5.0 (6.4)	0.5 (0.6)	2.2 (2.8)	5.2 (6.4)	3.3 (6.1)	5.4	0.0467	0.40	**0.0678**	**0.021**
Average (1–4)	384 ± 308	96.5 ± 104.5 (140.2 ± 124.1)	50.3 ± 51.0 (72.1 ± 66.9)	1.1 ± 0.6 (1.4 ± 0.9)	6.6 ± 4.6 (8.5 ± 5.5)	14.8 ± 8.3 (18.3 ± 9.1)	9.3 ± 8.0 (14.1 ± 7.6)	5.4 ± 0.8	0.0220 ± 0.019	0.44 ± 0.15	0.0418 ± 0.018	0.11 ± 0.15
All other springs	1287 ± 722	8.1 ± 15.2	5.8 ± 8.2	1.0 ± 0.8	3.9 ± 1.8	11.3 ± 10.5	6.3 ± 5.8	6.1 ± 0.9	−0.0055 ± 0.030	0.41 ± 0.33	0.0040 ± 0.031	0.42 ± 0.27

For the nutrient elements potassium (K^+), calcium (Ca^{2+}) and magnesium (Mg^{2+}) we found comparable, but less distinct patterns (Fig. 2d–f). Average concentrations of Ca^{2+} were 1.3 times higher for the salt impacted springs than for non-impacted springs (14.8 mg L^{-1} vs. 11.3 mg L^{-1}, U = 1408.0, p = 0.02). For Mg^{2+} we observed 1.7 times higher concentrations for salt impacted springs compared to the non-impacted springs (6.6 mg L^{-1} vs. 3.9 mg L^{-1}, U = 1401.0, p = 0.02). We observed no significant differences in the average concentrations of K^+ (1.1 mg L^{-1} vs. 1.0 mg L^{-1}, U = 1113.0, p = 0.28) between impacted springs and non-impacted springs. Similar to the maximum concentrations of sodium and chloride also the highest maximum concentrations of K^+, Ca^{2+} and Mg^{2+} were observed near the road and decreased with increasing distance to the road (Table 2). Temperature and discharge regime did not significantly differ between the four salt impacted springs and the other 48 non-impacted springs in the study area, which creates appropriate conditions for comparisons between these two groups of springs.

Focusing on the long-term temporal trends of hydro-chemical parameters for the salt impacted springs (1996–2013), a significant increase in chloride concentrations was observed for the spring closest to the road (spring 1: slope = 3.9 mg L^{-1} $year^{-1}$, p = 0.02). This temporal increase of chloride concentration was even more pronounced for the second closest spring to the road, although the trend was not significant (spring 2: slope = 6.9 mg L^{-1} $year^{-1}$, p= 0.12). The two other salt impacted springs showed no significant trends but rather constant concentrations over the whole monitoring period (slope = − 0.035 and − 0.08 mg L^{-1} $year^{-1}$ with p = 1.0 and 0.71, respectively, Fig. 2a). We observed no significant trends for concentrations of sodium (Na^+, slope = 0.99 ± 1.57 mg L^{-1} $year^{-1}$, p= 0.47± 0.37, n= 4) and potassium (K^+, slope= 0.02 ± 0.02 mg L^{-1} $year^{-1}$, p = 0.42 ± 0.1, n = 4). Concentrations of calcium significantly increased for the spring closest to the road (spring 1, slope = 0.44 mg L^{-1} $year^{-1}$, p < 0.001) but stayed constant for the three other springs (slope = 0.28 ± 0.32 mg L^{-1} $year^{-1}$, p = 0.42 ± 0.26, n = 3). The same

was true for the temporal trend in magnesium concentrations, which significantly increased for the spring closest to the road during the two decades of investigation (slope = 0.25 mg L^{-1} $year^{-1}$, p = 0.005) but stayed constant for the three other springs (slope = 0.17 ± 0.23 mg L^{-1} $year^{-1}$, p = 0.41 ± 0.25, n = 3). For detailed information about the long-term temporal trends of the investigated hydro-chemical parameters see Table A.1 (Appendix A).

Focusing on the long-term temporal trends for the recovery from acidification, none of the four monitored springs under salt impact showed a significant increase in pH values (measured in September) over the 25 years of investigation (slope = 0.022 ± 0.019 pH units $year^{-1}$ with p = 0.44 ± 0.16, see Table 2). However, when considering the acidity regime indicated by the plant community composition of the springs (via weighted Ellenberg indicator values), we observed a significant increase of community weighted indicator values, meaning a significant recovery from acidification for three of the four springs along the road but not for the highest salt-impacted spring (Table 2). Rates of recovery indicated by the plant community composition of the salt impacted springs increased with increasing distance to the road (Fig. 3). Furthermore, the plant community of the highest salt-impacted spring (spring 2) indicated a strong increase in acidity between 2004 and 2005 which goes along with a strong increase in concentrations of Na^+ and Cl^-, which was observed between 2003 and 2004 (see Figs. 2a and b and 3, respectively). Detailed information about the temporal change of plant community composition in the four salt impacted springs and the respective, species-specific indicator values for acidity are provided in the online Supplementary material (Appendix B).

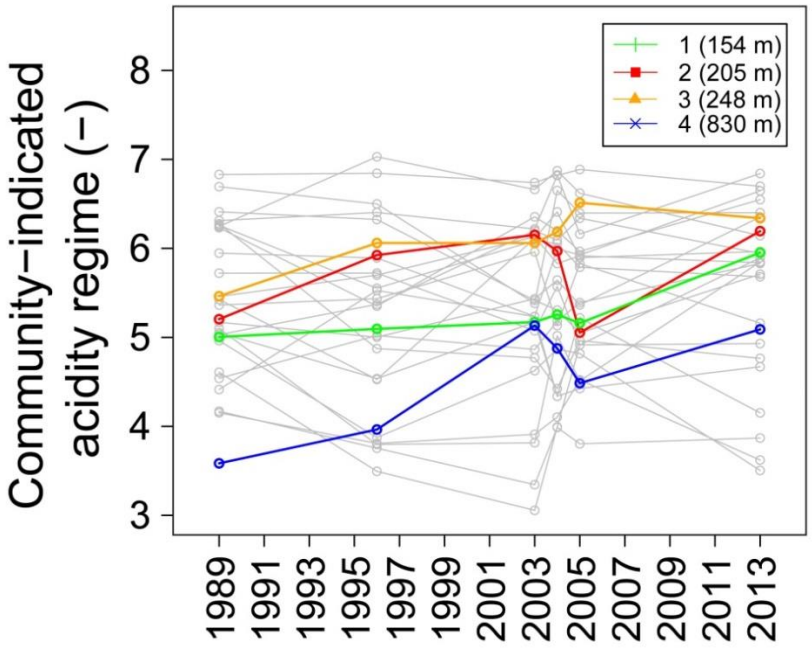

Fig. 3. Long-term trends of acidity regime indicated by plant community composition of forest springs lying in different distances offstream a state road with frequently road salt application during winter months. Salt-impacted springs are marked by coloured individually marked lines; non-impacted springs are depicted as grey lines (distance of the salt impacted springs to the road is depicted in parenthesis).

3.2. Seasonal dynamics in the water chemistry of salt impacted springs

Considering the seasonal variation in the hydro-chemistry of the salt impacted springs, we observed distinctive peaks in the water concentrations of sodium and chloride in April/May after winter seasons with high snow load (2003/04 and 2012/13) but not after winters with low snow cover (2013/14, see Fig. 4 for water concentrations and Fig. 5 for snow height). Generally, impact of road salt during the winter months resulted in high concentrations of Na^+ and Cl^- throughout the whole annual course (Cl^-: Fig. 4a and d; Na^+: Fig. 4b and e). Monthly measured pH values were mostly constant and the lowest throughout the season for spring 2 which also showed the highest road salt impact but pH increased in seasonal variation and absolute values with increasing distance to the road. Similar to the long-term trends, the spring closest to the road (spring 1) stood out with comparably low Cl^- and Na^+ concentrations but high pH values. The described patterns were true for the seasonal courses of 2003/2004 as well as 2013/2014.

For the nutrient elements potassium, magnesium and calcium we found no significant correlation between mean concentrations and seasonal variation of K^+, Mg^{2+} and Ca^{2+} ($p = 0.35$, 0.70 and 0.80, respectively). However, we observed the highest seasonal concentrations for the most salt impacted springs and decreasing concentrations with increasing distance to the road (K^+: Fig. A.1a and d, Mg^{2+}: A.1c and f and Ca^{2+}: A.1b and e, Appendix A). Furthermore, we found a very strong positive correlation between the monthly concentrations of Na^+ and K^+ measured during the seasonal courses of 2004/2004 and 2013/2014 (Pearson $r = 0.61$, $p < 0.001$). The correlation was even stronger for Na^+ and Mg^{2+} ($r = 0.70$, $p < 0.001$) and Na^+ and Ca^{2+} ($r = 0.80$, $p < 0.001$). This strong correlation between salt impact and concentrations of the nutrient elements was not observed for the seasonal courses of the control group of non-impacted springs ($n = 48$) ($r = 0.12$ for K^+, 0.24 for Mg^{2+} and 0.15 for Ca^{2+}).

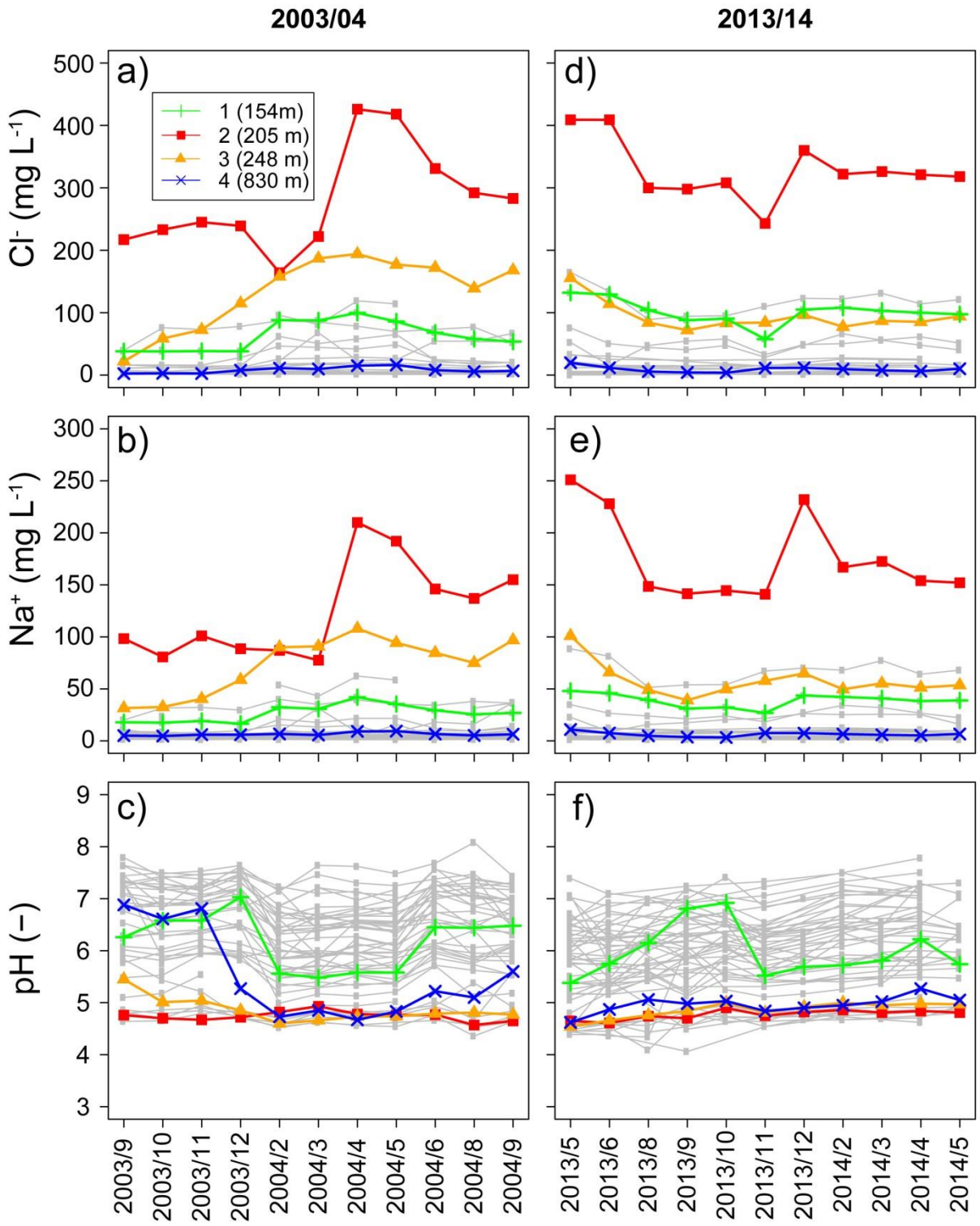

Fig. 4. Seasonal trends of concentrations of road salt related cations (a, b, d and e) and pH (c and f) measured in the water of forest springs lying in different distances offstream a state road with frequently road salt application during winter months. a–c: Seasonal course 2003/2004 (September to September), d–f: seasonal course 2013/2014 (May to May). Salt impacted springs are marked by coloured individually marked lines; non-impacted springs are depicted as grey lines.

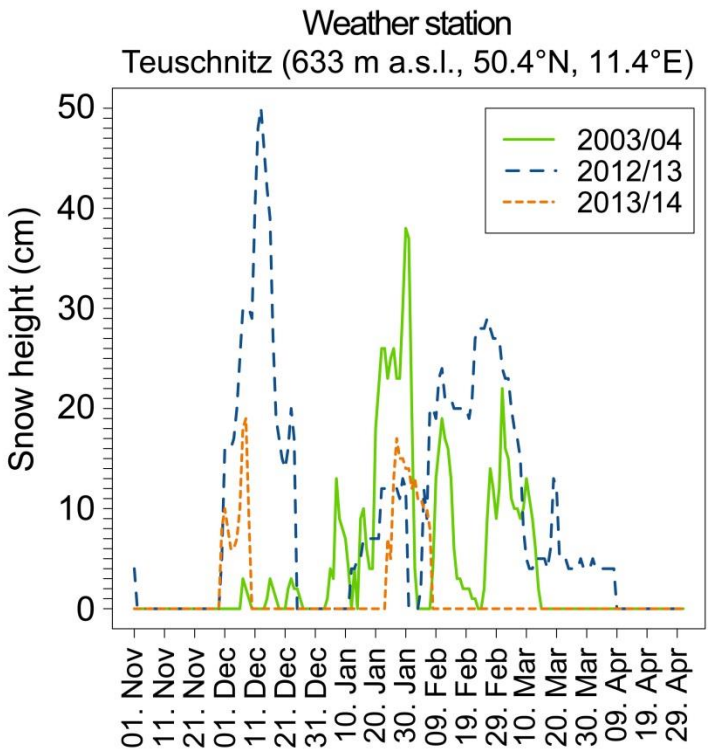

Fig. 5. Seasonal variation of snow height measured parallel to the seasonal water sampling during winters with high (2003/04, 2012/13) and low snow cover (2013/14). The location of the weather station is indicated in Fig. 1. Datasource: German weather service (DWD), weather station Teuschnitz.

4. Discussion

Various environmental factors are known to affect long-term recovery of anthropogenically acidified forest catchments including the 'sea salt effect' (Wiklander, 1975), with episodic sea salt input significantly hindering long-term recovery of coastal forest ecosystems (Larssen and Holme, 2006; Skjelkvåle et al., 2007; Laudon, 2008; Akselsson et al., 2013). By increasing the net charge in the soil solution, episodic input of sea salt is described by experimental as well as field studies to increase cation exchange processes in the soil, leading to temporary acidity flushes in the run-off especially in already acidified soils (Wiklander, 1975; Hindar et al., 1995; Skjelkvåle et al., 2007; Laudon, 2008). Furthermore, increasing concentrations of sodium are reported to enhance the leaching of important soil nutrients like K^+, Mg^{2+} and Ca^{2+} (Larssen and Holme, 2006; Findlay and Kelly, 2011; Akselsson et al., 2013). Although sea salt is chemically identical to the most widely used de-icing agent, namely sodium chloride (BayLfW, 1999; Green et al., 2007), ecological effects of road salt application are rarely tackled.

By conducting a long-term monitoring of water chemistry and plant community composition of forest springs over more than two decades, we were able to show a strong 'road salt effect' in Central European forest catchments. The application of road salt had not only significant seasonal but also long-lasting effects on the acidity regime and plant community composition of the investigated springs. On the

long run, but also on a seasonal time-scale, we observed the highest concentrations of chloride (Cl^-) and sodium (Na^+) for springs close to the salt emitting road. In accordance, measured pH values were the lowest for these highly salt impacted springs, whereas water concentrations of the nutrient elements potassium (K^+), calcium (Ca^{2+}) and magnesium (Mg^{2+}) were the highest. With one exception this 'road salt effect' decreased with increasing distance to the road, but was still detectable in 830 m distance from the road. The annual application of road salt during winter months, therefore, showed not only seasonal effects on the catchment chemistry and, thus, the hydro-chemistry of the investigated springs but also seems to cause on the long run a significant leaching of important nutrients (K^+, Ca^{2+} and Mg^{2+}) from the road adjacent, forested catchments. In combination with a road salt induced acidification, which was indicated by the temporal variation in plant community composition, continuous road salt application seems to continue the biogeochemical and subsequent ecological effects of historic acidification and, therefore impairs the long-term recovery of forested catchments and subsequent springs from historic acidification.

The observed effects of episodic road salt input on the long-term recovery of forested catchments seem to be, thus, comparable to the 'sea salt effects' observed by Wiklander (1975) in forests impacted by episodic airborne sea salt input. Significant long-term effects of episodic sea salt input were reported by Akselsson et al. (2013) with maximum concentrations for sodium in the soil water of 32 mg L^{-1} and for chloride of 59 mg L^{-1}. The maximum concentrations we measured in salt impacted springs for sodium (Na^+: 155 mg L^{-1}) and chloride (Cl^- :298 mg L^{-1}) not directly after the snowmelt but five months later (in September) are still five times higher, which underline the intensity of road salt contamination in our study. Due to the pedo- and geogenic conditions in the study area, which is mainly characterised by Cambisols on Pleistocene solifluction layers of argillaceous schist, road salt application is the only source explaining the high concentrations of sodium and chloride in the monitored springs.

A previous study on monitoring wells in the direct vicinity of German highways showed strong seasonal peaks of sodium and chloride between February and April (BayLfW, 1999). In our study, we observed strong seasonal peaks of both ions after winters with high snow loads during April/May (winter 2003/04 and 2012/13) but not after a winter with low snow cover (2013/14). Although several studies decline long-term effects of road salt application (e.g., Bay LfW, 1999), recent studies assume that winter-applied salt is not just rapidly flushing through the systems directly after snowmelt but remains in the systems for several months and, thus, harms ecosystems for an extended period of time (Findlay and Kelly, 2011). Our results clearly show that road-salt application not only causes distinctive peaks of Na^+ and Cl^- concentrations during the periods of snowmelt, but increases concentrations of both ions in the water of road adjacent springs over the full course of a year. As road salt is applied annually in high amounts during winter, high concentrations of sodium and their geochemical and ecological consequences can remain actively over decades.

Although we observed in general strong effects of road salt application on nutrient leaching, the desorption of cations caused by road salt application seems to vary among soil nutrients with stronger effects on magnesium than on calcium and potassium. With increasing atomic number as well as increasing ionic radius the probability of exchange increases for the exchangeable cations. The exchange

probability decreases in the order $Na^+ > K^+ > Mg^{2+} > Ca^{2+}$ (Scheffer and Schachtschabel, 2010). If the pool of one of the better exchangeable cations is exceeded, the cation with the next lower probability is likely to be exchanged. This seems to be exactly the case for road salt impacted springs in our study. Observed seasonal as well as long-term concentrations of potassium and calcium measured for salt impacted springs are comparable low whereas concentrations of magnesium are extraordinary high. Thus, the soil pool for potassium is likely to be already exceeded by exchange processes whereas magnesium is strongly mobilized. This explains the increased concentrations of K^+, Mg^{2+} and Ca^{2+} in the highly salt impacted springs. As magnesium and calcium are also minor ingredients of the de-icing agents (BayLfW, 1999), the increased concentrations of both cations which we observed in the highly salt impacted springs could also originate from the de-icing agent itself and not from cation exchange processes in the catchment soils. But in contrast to the seasonal peaks of Cl^- and Na^+ during periods of snowmelt, we did not observe these peak concentrations for K^+, Mg^{2+} and Ca^{2+}. Concentrations of all three nutrients stayed constantly high after the snowmelt event during the whole season. Thus, the increased concentrations of calcium and magnesium we observed for the highly salt impacted springs are rather caused by cation exchange processes in the catchments than by Mg^{2+} and Ca^{2+} originating as ingredients from the de-icing agent itself.

Although we observed no direct effect of road salt on the pH values measured for the monitored springs in September, we detected considerable differences in the long-term recovery rates for the acidity regime indicated by the monitored spring plant communities. We furthermore showed that the acidifying effect of road salt application is strongly reflected in the interannual response of spring inhabiting plant communities. In combination with the hydro-chemical measurements, we were therefore able to detect a significant long-term effect of road salt application by using this biomonitoring approach. At the first glance hydro-chemical measurements seem to be more precise compared to bioindication through plant species. However, plants growing in the investigated springs are permanently exposed to spring water. Thus, they must be adapted to the specific hydrochemical site conditions. And, it is not one single species that is referred to but whole species assemblages of the spring communities, which provide a large sample size and average values. Previous studies confirm that the occurrence and abundance of plant species, which inhabit spring habitats, is strongly related to the spring water chemistry and especially to the pH of the groundwater discharge (Audorff et al., 2011; Kapfer et al., 2012). Monitoring of established spring plant communities, thus, allows a temporal integral of environmental conditions that may not be reflected during a survey within an individual campaign of hydro-chemical measurements.

A high vulnerability of acidified catchments to episodic sea salt input has been documented (Hindar et al., 1995; Larssen and Holme, 2006). As large parts of Central Europe experienced high loads of acidifying pollutants during the 1970s and 1980s (Alewell et al., 2000), the ‘road salt effect’ which is shown here to hinder the long-term recovery of acidified forest ecosystems is especially relevant for this region. However, road salt contamination does not seem to affect recovery rates as a single independent factor but rather to interact with other factors like agricultural land-use in the catchments. This explains the low concentrations of sodium and chloride but high pH values we measured for the water of the spring closest to the road. In contrast to other monitored road springs where more than 70% of each catchment is covered with coniferous forest, the catchment of this spring shows a visible higher portion of agricultural

area in the catchment (see Table 1). This agricultural area is located between the road and the spring in the off stream. Parallel to the significantly higher pH values we observed significantly elevated concentrations of nitrate (NO_3^-), which might originate from this agricultural area. High inputs of sodium have been shown to significantly disrupt the nitrogen cycle in road adjacent soils by increasing the release of ammonium to the soil solution (Green and Cresser, 2008; Findlay and Kelly, 2011). By increasing the availability of ammonium for microbial processes such as nitrification, road salt is reported to increase nitrogen leaching form roadside soils and, thus, cause high loads of nitrate in the downstream aquatic systems (Green et al., 2007; Green and Cresser, 2008; Findlay and Kelly, 2011), which goes along with our observations.

In addition to this interactive effect of agricultural practice and frequent road salt application, other factors seem to affect acidification recovery in the study area as well. Temporal trends of measured and indicated acidity show considerable variation among all springs investigated in the study region. Forest management and in particular intensified forest management (Hultberg and Ferm, 2004; Akselsson et al., 2013) as well as extensive clear cutting (Nykvist and Rosén, 1985; Piirainen et al., 2004) and intensification of spruce cultivation (Larssen and Holme, 2006) are found to increase the mobilisation of acidifying cations and important nutrients. But also increasing temperatures will enhance nitrification and subsequent leaching of nitrate, increasing the risk of both, eutrophication and further acidification of forest systems that are already under stress (van Breemen et al., 1998; Wright and Jenkins, 2001; Akselsson et al., 2013). Also the increasing frequency and intensity of climatic extreme events like extensive drought periods very likely synergistically interact with acidification related stressors (Laudon, 2008; Akselsson et al., 2013). We therefore need to fully understand the interaction of abiotic and biotic factors jointly affecting the recovery of acidified forest ecosystems.

5. Conclusions

By conducting seasonal and also long-term monitoring of water chemistry and plant community composition of springs over two decades, we show that high loads of road salt input significantly suppress the long-term recovery of forested catchments from previous acidification. As increasing evidence stresses the widespread and persistent adverse effects of current de-icing practice, the call for alternatives becomes ever louder. While most alternative strategies including novel, more eco-friendly de-icing agents are expensive or might have other unclear environmental consequences, adjustments in the management of road salt application rates and times are required. Action must be taken now to stop rubbing salt into the ecological wounds caused by the anthropogenic acidification of forest ecosystems in the past and the ongoing, extensive application of road salt.

Acknowledgements

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Appendix A

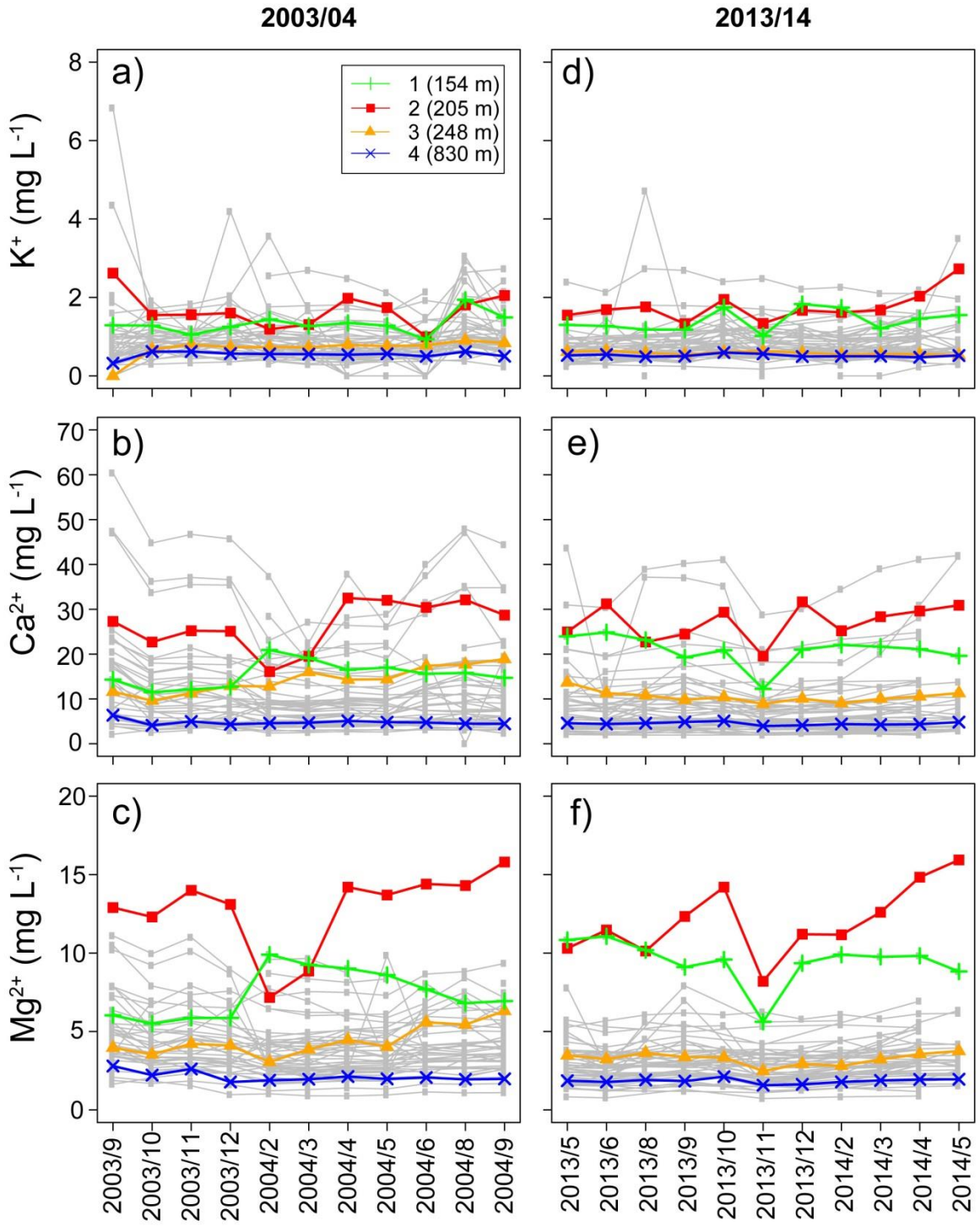

Fig. A.1. Seasonal trends of concentrations of important nutrient elements measured in the water of forest springs lying in different distances offstream a state road with frequently road salt application during winter months. a–c: Seasonal course 2003/2004 (September to September), d–f: seasonal course 2013/2014 (May to May). Salt impacted springs are marked by coloured individually marked lines; non-impacted springs are depicted as grey lines.

Table A.1. Long-term trends in hydro-chemical parameters measured in the water of forest springs lying in different distances offstream a state road with frequently road salt application during winter months. Shown are slopes and p values of ordinary least squares regression models (based on September measurements of water chemistry between 1996 and 2013).

		Na^+ [mg L^{-1}]		Cl^- [mg L^{-1}]		K^+ [mg L^{-1}]		Ca^{2+} [mg L^{-1}]		Mg^{2+} [mg L^{-1}]		NO_3^- [mg L^{-1}]	
Spring	Distance to road [m]	slope	p-value	slope	p-value	slope	p-value	slope	p-value	slope	p-value	slope	p-value
1	154	1.01	0.094	3.88	0.023	0.03	0.293	0.44	0.001	0.25	0.005	-0.63	0.065
2	205	3.21	0.31	6.86	0.121	0.04	0.439	0.64	0.122	0.44	0.131	-0.39	0.309
3	348	-0.18	0.958	-0.04	0.996	0.01	0.533	0.14	0.635	0.05	0.603	-0.24	0.336
4	830	-0.08	0.504	-0.08	0.713	0.01	0.402	0.05	0.492	0.03	0.503	-0.19	0.429

Appendix B. Supplementary data

Supplementary data to this article can be found in the online version of this dissertation as well as online at: http://dx. doi.org/10.1016/j.scitotenv. 2015.06.034.

5.4 Manuscript 4

The ecological legacy of 20th century acidification carried on by ecosystem engineers

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Abstract

Question(s): Acidification by airborne pollution strongly degraded terrestrial and aquatic ecosystems until the late 20th century. Although geochemical recovery is observed since then, recovery of ecological communities still fails to appear with unclear causes. Joint effects of anthropogenic pollution and biogenic habitat modification by ecosystem engineering species are thereby neglected so far. Here we hypothesize, that positive feedbacks between past anthropogenic acidification and the ongoing, biogenic habitat modification by peat moss species (genus *Sphagnum*) will significantly affect the plant community composition of acidified spring fens on a decadal scale.

Location: Spring fens located in the forest landscapes of Central Germany's siliceous mountain ranges. These spring fens were impacted by anthropogenic acidification until the late 1980s and showed strong increases in dominance of *Sphagnum* species during the last 25 years of investigation.

Methods: Vegetation surveys (vascular plants, mosses and liverworts) and hydro-chemical water measurements of 54 spring fens over a study period of 25 years (1989-2013). Measurements of water pH and discharge were used in combination with Ellenberg Indicator values of the occurring plant species to investigate the joint effect of anthropogenic acidification and biogenic habitat modification by *Sphagnum* species.

Results: Changing plant communities (excluding *Sphagnum* spp.) indicated significant increases in acidification for spring fens with high *Sphagnum* cover although pH measured for the outpouring groundwater showed no temporal trend. Increasing A path analysis revealed significant enhancing effects of *Sphagnum* abundance on the community-indicated acidity regime which was independent from the abiotic acidity regime (water pH). With increasing species richness trough time, community assemblies became increasingly similar and shifted towards acid tolerant species. Characteristic plant species of non-acidified spring fens like *Chrysosplenium oppositifolium* were replaced by generalist grass, sedge and tree species from surrounding forest communities (e.g. *Picea abies*, *Fagus sylvatica*, *Calamagrostis villosa* and *Carex remota*).

Conclusions: Based on long-term monitoring data we show that combinations of historic anthropogenic and ongoing biogenic habitat modification can significantly change plant community composition. These complex functional legacies, which are shown here to be active over decades, stress the importance to consider the history and memory of ecosystems in global change impact research.

Key words

air pollution; alternative stable states; ecological memory; hydrochemistry; physical ecosystem engineers; restoration, tipping points; vegetation

Nomenclature

Jaeger (2011) for vascular plants; Frahm und Frey (2004) for mosses

Introduction

The acidification of ecosystems caused by airborne pollutants has to be considered as one of the most serious environmental problems associated with industrialization (Bouwman et al., 2002; Narita et al., 2012). During the second half of the 20th century, terrestrial ecosystems of Central Europe and North America were heavily impacted by atmospheric acid emissions during the mid-1960s to 1980s (Cowling 1982; Gorham 1998). Acid depositions characterized by sulphuric and nitric acids had profound, detrimental effects on forest ecosystems and their whole catchments including soils and water bodies with strong implications for ecosystems' functioning and services (Skjelkvåle et al. 2001; Johnson et al. 2008).

Large-scale forest decline as a detrimental consequence of airborne pollution provoked strong public attention during that time and acidification was actively discussed in scientific literature until the mid-1990s (Johnson et al. 2008). Decreasing conspicuity of the ecological effects of acidification led to a marked decrease of political and scientific interest in this topic during the last decade (Kopittke et al. 2012). However, biological recovery from past anthropogenic acidification is reported just exceptionally and seems to be far from reaching previous conditions although the initial source of acidification, namely airborne pollution was tremendously reduced in Europe and North America at the end of the 20th century (Ormerod & Durance 2009; Holmgren, 2014; Malcolm et al. 2014).

Disagreement exists about the causes of restricted ecological recovery with several potential drivers being proposed, including geochemical legacies (Oulehle et al. 2006) and multiple intervening environmental stressors such as climatic extreme events (Holmgren 2014). However, understanding about the ecological long-term response to acidification is more important than ever, as acidification of terrestrial ecosystems still continues on even larger scale in emerging nations of Asia, Africa and South America. Countries like China, which experience fast economic growth, actually face immense environmental challenges such as forest dieback and loss of biodiversity in particular in marine and freshwater ecosystems due to accelerating acidification with detrimental implications on the ecological services and human well-being on continental scale (Stoddard et al. 1999; Guo et al. 2010; Lu et al. 2010).

The question about the continuing ecological effects of previous anthropogenic acidification is especially relevant as an increasing understanding of ecological systems and processes indicates that the response of most ecological systems to a certain environmental stressor is not linear (successional) but is characterized by tipping points, non-linear dynamics and alternative stable states which can arise or be sustained by positive or negative feedbacks between abiotic and biotic system elements (Sutherland 1974; Scheffer & Carpenter, 2003; Fung et al. 2011). In general, ecosystems have to be considered as temporally dynamic systems shifting discontinuously between alternative stable states, meaning different sets of possible conditions like e.g. different species assemblages.

This idea of non-linear dynamics leading to alternative stable states in ecosystems was established in the 1970s (Holling 1973) and is widely accepted in ecology and nature conservation practice (Capon et al. 2015; Kéfi et al. 2015). System shifts can be triggered by external forces like anthropogenic acidification. Depending on the inherent system stability as well as the strength of the triggering force, ecosystems can either compensate the stress which is induced by the trigger and stay in the current state or

shift to a new state if the trigger pushes the system across a certain tipping point (Beisner et al. 2003). Once a system shifted to a new state, positive feedbacks between abiotic environmental conditions and biotic system elements (i.e. species) can further stabilize the new system state.

Especially ecosystem engineers (i.e. species that modify environmental settings and, thus, resource availability for other species; Jones et al. 1997) are likely to stabilize ecosystems in new, alternative states after a system shift was induced by abiotic perturbation (Hagerthey et al. 2008). Engineering species, which are initially favoured under anthropogenic impact can further modify habitat conditions, with favourable or unfavourable consequences for the other, co-occurring species, resulting in persistent shifts in the composition of ecological communities (van Breemen 1995; Granath et al. 2010). Such interactions between abiotic environmental triggers and ecological engineers affecting the whole community composition are reported for freshwater ecosystems (eutrophic, shallow lakes; Scheffer 1989), marine ecosystems (coral reefs; Fung et al. 2011) and semi aquatic ecosystems (fen-bog transition; van Breemen 1995; Granath et al. 2010).

Despite these striking examples, positive feedbacks between anthropogenically altered abiotic habitat conditions and ecosystem engineering species are neglected so far as a potential cause for the delayed ecological recovery from historical acidification. This is surprising as ecosystem engineers are assumed to influence ecosystem dynamics and, thus, have influence on ecological response trajectories in almost every ecosystem on earth (Jones et al. 1997).

Here we specifically tackle positive feedbacks between an abiotic trigger and habitat modulating species by studying the long-term response of plant communities to the 20th century anthropogenic acidification. We therefore focus on Central European softwater spring fens with forested catchments on siliceous parent material which were heavily impacted by historic acidification. In these ecosystems peat moss species (genus *Sphagnum*), which are reported by numerous studies to be favoured by anthropogenic acidification (Bayley et al. 1987; Rochefort et al. 1990, Ek et al. 1995), showed strong increases in dominance during the last 25 years although acidifying emissions and, thus, deposits decreased substantially during that period of time.

Peat mosses are known to be key ecosystem engineers who actively acidify their environment by cation exchange processes related to nutrient uptake and, thus, force the co-occurring species to either adapt or make way for other species as site conditions change (van Breemen 1995; Bragazza 2006). A positive feedback between past anthropogenic acidification and the ongoing, biogenic habitat modification by increasing peat moss abundance seems therefore likely to continue the legacy of anthropogenic acidification. We therefore hypothesize, that this positive feedback between abiotic and biotic system elements continuously shift plant community composition of acidified spring fens towards even more acidophilous assemblages. To test this hypothesis, we compared long-term measured trends (25 years) of abiotic environmental conditions with those indicated by plant community composition for 54 spring fens located in the forest landscapes of Central Germany's siliceous mountain ranges.

Methods

Study sites

We studied spring fens (n = 54) in the forested, mountainous landscapes of Central Germany (lat. 49.9–50.6 °N, long. 11.2–12.2 °E, Fig. 1). Due to the dense bedrock overlain by Pleistocene solifluction layers, all investigated spring fens are fed by near-surface groundwater leading to constant but rather low discharge rates (mainly below 2 L s^{-1}). Therefore, geochemical effects of anthropogenic stressors like airborne acidification, climatic warming or land use change, which occur in the forested catchments, can be detected by studying the water characteristics and plant community composition of these systems.

The forested catchments feeding the investigated spring fens are characterized by Norway spruce (*Picea abies* (L.) H. Karst) partly intermixed with European beech (*Fagus sylvatica* L.) (Schweiger & Beierkuhnlein 2014). The investigated spring fens are characterized by a few to some hundred square meters large seepage area where the feeding groundwater discharge diffusively seeps out from the ground. Plant communities of pristine spring fens are limited to this precise location and differ considerably from surrounding forest floor species assemblies.

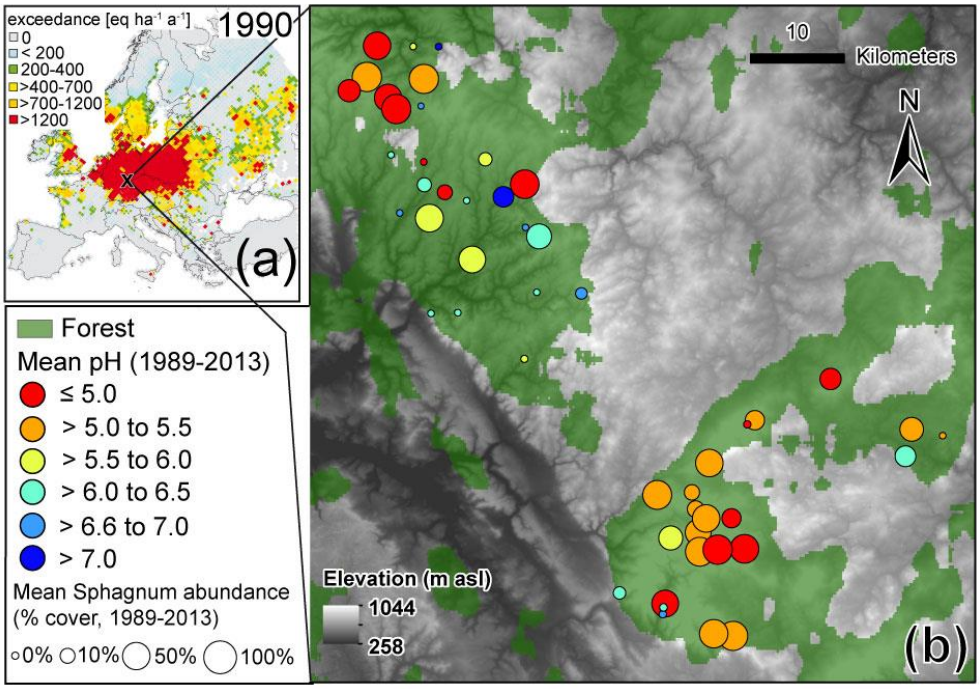

Figure 1: Patterns of 20th century acidification and its long-term consequences in Central European spring fens. (a) Average accumulated exceedance of critical loads for acidification for 1990 (acidifying potential of the deposited air pollutants in a particular ecosystem in acid equivalent per ha and year, modified from the EEA Technical report 11/2014; for more detail see European Environment Agency 2014). (b) Patterns of pH-values and *Sphagnum* cover of spring fens (n = 54) in the lower mountain ranges of Central Germany (study period 1989-2013). Mean pH of the groundwater discharge is visualized by different colours (red: low pH to blue: intermediate pH). Mean abundance of *Sphagnum* mosses (% cover) is visualized by different point sizes.

The forested catchments feeding the studied spring fens experienced high loads of acidifying pollution during the peak emission times between the 1970s and 1990s (Fig. 1). Furthermore, siliceous bedrock (schists and granite) which is dominating the study region features low geogenic buffering capacity against atmospheric acidification which was strongly exhausted during periods of peak emissions. The combination of both facts (high loads and low buffering) led to strong acidification of forested catchments and the subsequent, aquatic ecosystems (including the studied spring fens) in the studied region during the 1970s to 1980s (Matzner & Murach 1995).

Data collection

Data collection for this study started right after legal regulations to reduce acidifying pollution were introduced in western countries in the 1980s and exactly with the breakdown of East German and Czechoslovakian air polluting industry. This timing enabled us to study ecosystem responses to improved environmental conditions at a decadal scale.

Since 1989, we investigated plant community composition and hydro-chemical water characteristics related to acidification. This was done with high spatial resolution for spring catchments in four intense measuring periods during the 25 years of investigation (1989, 1996, 2003 and 2013). We determined all vascular plants, mosses and liverworts growing in the water saturated seepage area during July or August of the study years (1989, 1996, 2003 and 2013) and estimated species cover using a modified Braun-Blanquet method (see Schweiger & Beierkuhnlein 2014). Water was sampled in September at the uppermost point of the spring sites where water seeps out of the ground to quantify the hydro-chemical conditions affected by anthropogenic acidification in the catchments but to exclude biogenic effects induced by habitat modification in the spring fens. Exhalation of CO_2 can for instance modify water pH instantly after seeping out to the surface. Furthermore, cation exchange processes related to the occurrence of *Sphagnum* can modify the pH. During sampling we measured water pH using a portable pH-conductivity multimeter (WTW pH/Cond 340i, Wissenschaftlich-Technische Werkstaetten GmbH, Weilheim, Germany). Water discharge of the total spring area was estimated based on a seven-point ordinal scale, ranging from 0 to >1.5 L s^{-1}.

Data analyses

Besides the measured physico-chemical spring water characteristics unaffected by biotic modification e.g. by eco-engineering species, we quantified long-term trends of the prevalent environmental conditions indicated by the plant community via Ellenberg indicator values (Ellenberg et al. 2001) of the occurring plant species. Therefore, species that occurred in more than 5% of the investigated spring fens were included in the analyses. As we were particularly interested in the ecosystem engineering potential of *Sphagnum*, all *Sphagnum* species detected in the study were excluded from the quantification of

community-indicated environmental conditions. Subsequently, a mean indicator value for acidity and moisture was calculated for all years and for each investigated spring fen based on the species-specific indicator values (excluding *Sphagnum* species) weight by the abundance of corresponding species (% cover) which occurred in the particular spring fen.

To quantify temporal variation in plant community structure we calculated the dissimilarity of community composition between spring fens through time based on the Bray-Curtis dissimilarity measure. Furthermore, Pielou's evenness was calculated based on the Shannon diversity for the plant communities of all spring bogs and years. For both calculations all species which occurred in more than 5% of the investigated spring fens were considered (with *Sphagnum* species for dissimilarity and with and without *Sphagnum* for Evenness calculations).

Temporal trends of measured and community-indicated acidity regime were tested by using simple linear regression models under consideration of the statistical requirements of the models. Furthermore, we conducted path analysis to disentangle the effect of acidity which is exclusively linked to catchment processes (pH of the outpouring groundwater) from acidifying effects related to the biogenic habitat modification by occurring *Sphagnum* species on spring plant community composition. In this path analysis we assumed an effect of groundwater acidity on both *Sphagnum* abundance and community-indicated acidity (excluding *Sphagnum*). Furthermore, we postulated a direct effect of *Sphagnum* abundance on the community-indicated acidity which depends on the eco-engineering potential of these species but is independent from the abiotic acidity regime of the feeding groundwater. In the partial least square based approach which was used to conduct the path analysis (plspm-R-package; v.0.4.1; Sanchez et al. 2013), direction and strength of potential effects were quantified by path coefficients (pc), which can be seen as an analogue to correlation coefficients of e.g. the Pearson correlation. All analyses were conducted in the R environment (v. 3.0.2; R Core Team 2013) with a level of significance of alpha=0.05.

Results

Long-term changes in plant community composition indicated a significant increase in acidity (based community-weighted Ellenberg indicator values for acidity, adj.R^2=0.13, $p<0.001$, Fig. 2) although acidity measured for the outpouring groundwater showed no significant change through time (adj. R^2= 0.0, $p>0.9$ for pH, Fig. 3a). Community indicated acidity visibly increased for spring fens with high *Sphagnum* cover during the 25 years of observation although pH measured for the outpouring groundwater slightly increased for those springs (see Fig. 2).

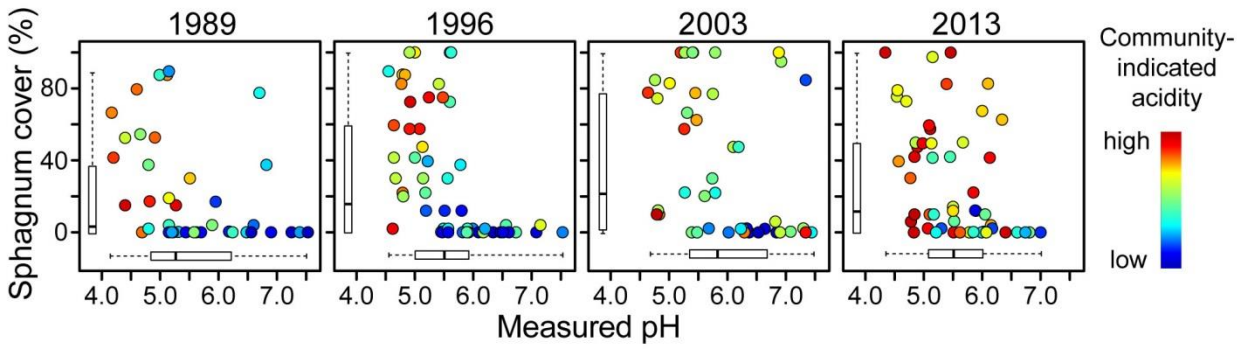

Figure 2. Long-term trends of peat moss abundance and measured as well as plant community indicated acidity in Central European spring fens. Boxplots and points depict peat moss cover and measured pH values of the outpouring groundwater at four time steps between 1989 and 2013. Acidity indicated by plant community composition is depicted in different colours (based on community-weighted Ellenberg indicator values for acidity with peat moss species excluded).

With increasing species richness (adj.R^2=0.35; p<0.001), community assemblies of the spring fens became increasingly similar through time (decreasing Bray-Curtis dissimilarity, adj.R^2=0.03, p<0.001) and shifted towards acid tolerant species (Fig. 3b and c). On individual species level, seedlings of two tree species (*Picea abies* (L.) H. Karst. and *Fagus sylvatica* L.) showed the strongest increase in abundance between 1989 and 2013, followed by the grass *Calamagrostis villosa* (Chaix ex Vill.) J. F. Gmel., the sedge *Carex remota* L. and seedlings of *Acer pseudoplatanus* L. (Fig. 4). Strongest decrease in abundance was observed for *Chrysosplenium oppositifolium* L., a characteristic species of pristine spring bogs in Central Europe. Evenness in community composition did not significantly change through time (including *Sphagnum*: p=0.39 and without *Sphagnum*: p=0.78).

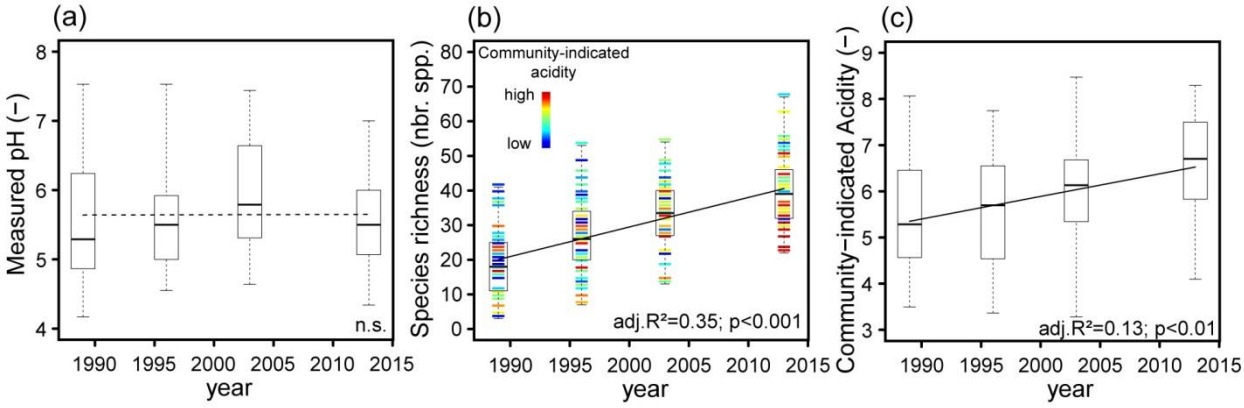

Figure 3: Long-term trends of species richness and measured as well as plant community indicated acidity in Central European spring fens. (a) pH measured for the outpouring groundwater (unaffected by biotic habitat modification). (b) species richness (community-indicated acidity is depicted by coloration for each spring site / year). (c) community indicated acidity. Solid line indicates significant; dashed lines non-significant temporal trends (n=54 springs investigated at each of the 4 time steps between 1989 and 2013).

Besides the indicated increase in acidity, changing plant communities indicated a significant decrease in moisture (based community-weighted Ellenberg indicator values for moisture, adj.R^2=0.31, p<0.001), although measured discharge showed no significant change over the 25 years of observation (p=0.67).

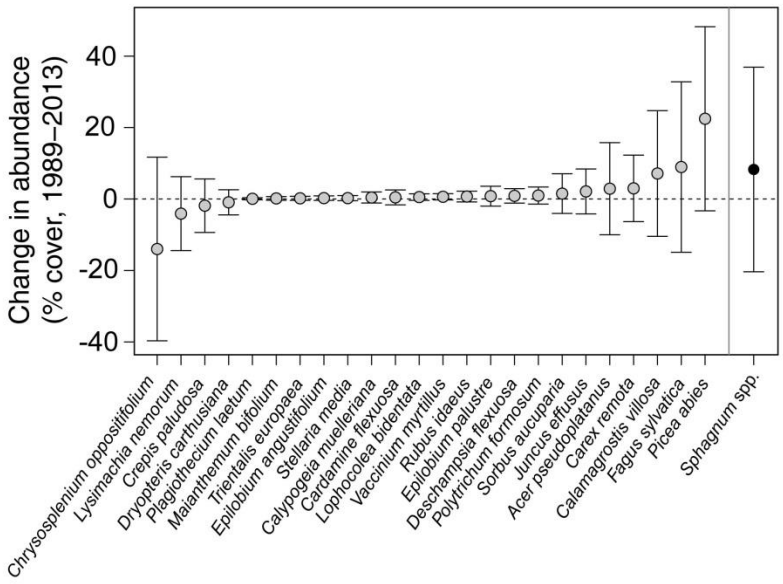

Figure 4: Long-term trends of abundance of peat moss and co-occurring plant species in Central European spring fens. Shown is the difference in species abundance between 1989 and 2013, points depict the arithmetic mean whereas error bars indicate the standard deviation for peat moss species (*Sphagnum* spp., black point) and co-occurring plant species (grey points, only shown for species with significant temporal trends over the full study period, 4 time steps, n= 54 spring fens).

Measured acidity regime, which was unaffected by biotic modification (pH of the outpouring groundwater), showed similar effects on both, the temporal development in *Sphagnum* abundance and the composition of the remaining plant communities. *Sphagnum* abundance as well as the acidity regime which was indicated by the composition of the remaining plant communities increased with increasing measured acidity (decreasing pH measured for the outpouring groundwater, path coefficient pc = -0.4 and -0.42, respectively, p<0.001 in both cases, Fig. 5a). The direct effect of water pH on plant community composition and, thus, community indicated acidity was thereby visible stronger than its indirect effect via *Sphagnum* abundance (see Fig. 5b, second bar).

Independent from the direct and indirect effect of the measured water pH on the plant community composition, increasing *Sphagnum* abundance additively affected community assembly by significantly shifting the remaining plant communities towards more acid tolerant species (pc = 0.23, p<0.001). In other words, *Sphagnum* abundance had a significant effect on plant community composition and, thus, on the community-indicated acidity regime, which was independent from the abiotic acidity regime i.e. the measured water pH (blue arrow in Fig. 5a and third bar in Fig. 5b).

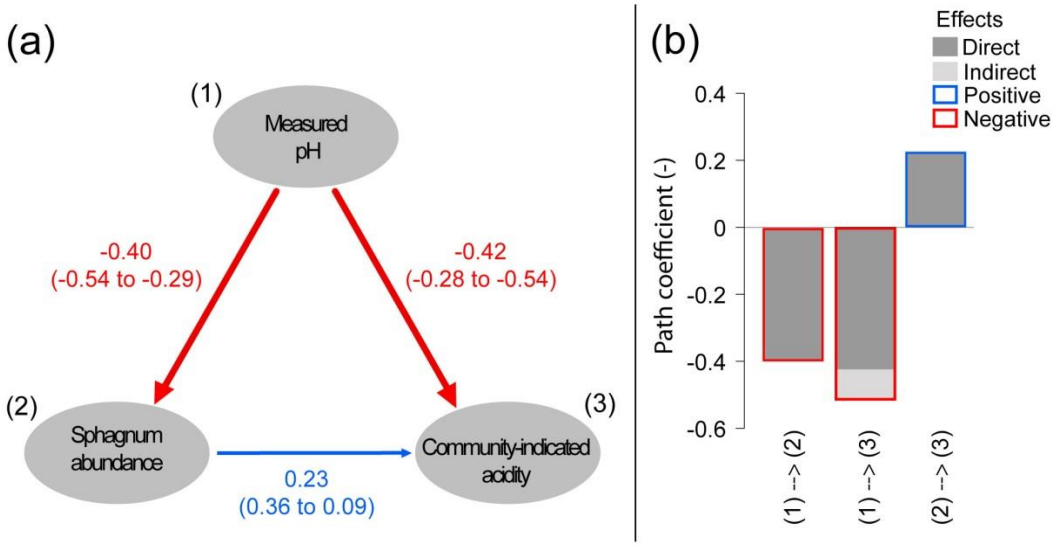

Figure 5. Effects of anthropogenic acidification and biogenic habitat modification on the plant community composition of Central European spring fens. (a) Effect of pH measured for the outpouring groundwater (unaffected by biogenic habitat modification, 1) and abundance of peat moss species (*Sphagnum* spp., 2) on the plant community composition in terms of indicated acidity (excluding peat moss species). Numbers depict mean as well as the 0.95 confidence interval (in parenthesis) of path coefficients which quantify abiotic / biotic effects on plant community composition (blue: positive and red: negative effects). Effects are divided in direct and indirect effects in (b).

Discussion

Our results show that ecosystem engineers like peat moss species of the genus *Sphagnum*, which are globally distributed (Shaw et al. 2003) can significantly modify the composition of co-occurring plant species and, thus, affect ecosystem functioning and service provision. Although ecosystem engineers are proposed to be important modulating system elements in almost every ecosystem on earth (Jones et al. 1997), the interactive effect of large-scale environmental stressors like atmospheric pollution and the modifying activity of ecosystem engineers on the response characteristics and biotic structure of ecosystems has been rarely tackled so far (but see Dorrepaal et al. 2006).

Here we show that historic anthropogenic acidification during the 20th century in combination with acidifying mosses of the genus *Sphagnum* can affect the acidity regime in semi-aquatic ecosystems on a decadal scale. Based on investigations on water chemistry and plant community composition of Central European spring fens over 25 years, we observed a significant increase of acidic conditions indicated by plant community composition whereas acidity of the outpouring ground water feeding the spring fens showed no sign of recovery or further acidification. At the same time *Sphagnum* species, as well-known ecosystem engineers in terms of biogenic acidification (Kooijman & Baker 1994; van Breemen 1995), increased in abundance during the 25 year time-series. Testing these observations with a path analysis to separate effects of abiotic and biotic acidification on the plant community response, we show that biogenic

acidification caused by increasing *Sphagnum* abundance in combination with the acidic environmental background can explain the observed shift of plant communities towards acidophilous species.

Sphagnum species which were reported to increase abundance under acidified conditions (Bayley et al. 1987; Rochefort et al. 1990, Ek et al. 1995) are well known for their capability to actively acidity their environment and, thus, force the co-occurring species to either adapt or make way for other species (Kooijman & Baker 1994; Hájek & Vicherová 2014). Besides their ability to actively acidify their environment, *Sphagnum* species are known to form thick carpets of plant tissue in fens which enhance the insulation from the water saturated ground (Bragazza 2006). In combination with the low decomposition rates of dead plant material which can be caused by the acidic conditions, this may create not only more acidic but also drier conditions on the surface that favour the establishment of other species. Besides the indicated shift towards more acidic conditions the changing communities also indicated decreasing soil moisture although we observed no significant trend in water discharge of the investigated spring fens through time. Comparable observations were made by Bragazza (2006) in a *Sphagnum* dominated mire in the south-eastern Italian Alps, where the biogenic lowering of the water table by peat accumulation lead to an increasing abundance of more drought tolerant, acidophilus ericaceous shrubs whereas more drought intolerant species of the initial community shifted their niche to the remaining places with a connection to the water saturated ground.

Both facts, increasing acidity as well as the decreasing moisture of substrate can favour species which were not characteristic for the initial spring communities but can cope with the novel, biogenically altered environmental conditions caused by an increasing abundance of *Sphagnum*. Analysing the temporal development of plant community composition, we found an immigration of species from neighbouring forest habitats. With increasing species richness through time, characteristic plant species of non-acidified spring fens like *Chrysosplenium oppositifolium* (Beierkuhnlein 1999; Schweiger et al. 2015) were replaced by generalist grass, sedge and tree species from surrounding forest communities (e.g. *Picea abies*, *Fagus sylvatica*, *Calamagrostis villosa* and *Carex remota*). Very likely these generalists were indirectly favoured by the decline of sensitive characteristic species as a result of the biogenic habitat modification, which causes both an increase in acidity and a decrease in surface moisture. Especially the establishment of tree species like *Picea abies* or *Fagus sylvatica* will have significant, additional effects on the acidity and moisture regime and, thus, on the plant community composition of the investigated spring fens.

In this study we show that strong interactions occur between a past anthropogenic stressor namely acidification and ecosystem engineering moss species of the genus *Sphagnum*. The combination of anthropogenic and biogenic modification of the acidity and moisture regime significantly changed plant community composition of the investigated spring fens on a decadal scale. By comparing both, long-term trends of measured abiotic conditions and of environmental conditions indicated by plant community composition we could underline the importance of temporally and spatially integrating, biotic information related to the indicatory value of plant species. These biogenic values enable another perspective compared to snapshot measurements of abiotic conditions. Considering the complex interaction of abiotic and biotic system elements jointly modifying ecosystem responses on decadal scale, ecosystem's history

and memory is a prerequisite to be accounted for in future projections on ecological effects of large scale environmental changes.

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Author Contributions

A.H.S. and C.B. conceived the idea; A.H.S conducted the analyses and led the writing process while C.B. revised the whole manuscript.

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5.5 Manuscript 5

Scale-dependence of temperature as abiotic driver of species distribution

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Abstract

Aim: Scale-dependence of patterns and processes is one of the major topics ecologists still have to struggle with. Ecosystem responses to environmental stressors are believed to be strongly scale-dependent. However, projections about future climate change effects on the spatial distribution of biodiversity are still restricted to certain scales with lacking knowledge about scale-dependence. Here we propose that strong cross-scale links between micro- and macro-environmental drivers and low environmental noise on small spatial scale will go along with high-cross-scale similarity (low scale-dependence) of species realized temperature niches, one of the most relevant ecological habits related to climate change.

Location: The investigations cover seven orders of magnitude of spatial scale ranging from local (below metre) and regional (kilometre) scale investigations in Central European wetland ecosystems to several thousands of kilometres by studying species' distribution on continental scale.

Methods: We combined information of species spatial occurrence (vegetation records on local and regional scale, digitalized distribution maps on continental scale) with information about the corresponding temperature regime of vascular plant species occurring in environmentally stable, wetland ecosystems characterized by tight cross-scale links micro- and macroclimatic conditions.

Results: We observed high cross-scale similarity of species temperature niche characteristics across the seven orders of magnitude of investigated spatial scale. However, the importance of temperature as abiotic driver decreased non-linearly with decreasing scale, suggesting a higher importance of additional (biotic) drivers of species occurrence on small spatial scales.

Main conclusions: The species realized temperature niche seems to be a fundamental ecological habit with high cross-scale similarity at least for ecosystems characterized by high environmental stability and strong cross-scale links between micro- and macro-environmental conditions. By increasing general ecosystem understanding our results will help to improve niche-based species distribution modelling, one of the major assessment-tools for ecological climate change effects.

Keywords

environmental noise, non-linearity, scaling, species distribution modelling, spring fens, wet-land ecosystems

Introduction

The realisation of ecological patterns is strongly linked to the scale under focus (Hutchinson 1953; Wiens 1989; Levin 1992). We here define scale as a unit of space, time or organismic association in terms of grain size (resolution) and extent (c.f. Allen & Starr 1982; Turner 2001). Patterns are non-random signals which exhibit a structure on a certain scale of space, time or organismic association and, thus, a certain (detectable or non-detectable) message on this particular scale (c.f. Grimm *et al.* 2005). Whereas a certain pattern might be detectable at one scale, it might be not visible, hidden or not obvious at another. Furthermore, the emergence of a non-random pattern on a certain scale is strictly causal, means there must be an underlying reason which can strongly vary with scale. Thus, the interpretation of ecological patterns and their underlying processes, which is one of the main goals in ecology, is also strongly scale-dependent (Levin 1999). The detection of the relevant scales of inquiry is therefore of major importance for the detection and the interpretation of ecological patterns (Wiens 1989; Levin 1992). However, the inability to cope with scale-dependence of ecological processes and patterns still impedes the integrative description of ecosystems across spatial and temporal scales and, thus, hampers a general understanding of ecosystem functioning (Levin 1992; Levin 1999).

The debate on scale-dependence of ecological patterns and processes is now revived in face of the challenges which arise with the large-scale (even global) anthropogenic changes in environmental conditions and the subsequent, rapid ecological responses. To cope with these challenges, a conceptual approach towards a better understanding of ecological processes and interactions across a wide range of scales of space, time and ecological entities (from single cells to populations of species and whole ecosystems) is urgently needed and increasingly recognized (Levin 1992; Levin 1999; Peters *et al.* 2004; Nash *et al.* 2014; Menge *et al.* 2015). Non-linear interactions and feedbacks of ecological entities across scales are proposed to be essential to maintain ecosystem stability and, thus, ecosystem functioning against potentially disrupting stressors (Holling 1992; Levin 1999; Gunderson & Holling 2002). Important insurance mechanisms of ecosystems which maintain ecosystem functioning and service provisioning (functional redundancy among species, keystone species) have been proposed to be strongly intertwined with cross-scale interactions among ecological entities (Peterson *et al.* 1998).

However, cross-scale interactions in ecological systems are completely understudied and are still just sparsely used as model framework for ecological studies (e.g. hierarchical modelling frameworks in species distribution modelling, Pearson & Dawson 2003). Knowledge is especially sparse for species range size characteristics and the underlying drivers (but see Blackburn & Gaston 1998). Due to increasing anthropogenic pressure on global biodiversity, niche-based species distribution modelling has become an inevitable tool to assess the effect of changing environment on potential future distribution of species (Soberón & Nakamura 2009; Potter et al. 2013). Although these models based on the concept of the realized ecological niche are frequently used in global change research and assessment, they strongly vary in their scale of inquiry without considering scale-dependence or cross-scale interactions (Randin et al. 2006; Chase & Myers 2011; Austin & Van Niel 2011).

Strong interdependence exists between the spatial (and temporal) distribution of a given species and the characteristics (width) of its ecological niche (Pulliam 2000; Wiens 2011). The species ecological

niche is often refereed to be one of the most important and fundamental concepts in ecology (Chase & Myers 2011). The concept of ecological niches was introduced by Grinnell (1917) and Elton (1927) and was later on revisited and modified by Hutchinson (e.g. Hutchinson 1957). Hutchinson defines the fundamental niche of a species as an n-dimensional space of environmental conditions under which the species would be able to exists, whereas the realized niche refers to the environmental conditions under which a certain species actually co-exist with other, competing species. This concept of the species realized niche, which is based on the species environmental requirements by accounting at the same time for species competitive interactions, can be assessed by recording the species occurrence and related environmental characteristics and, thus, is strongly related to the spatial and temporal distribution of species.

The ecological niche of species is proposed to have a hierarchical structure as the importance of abiotic and biotic factors in influencing the niche and, thus, the distribution of species varies across scales. Abiotic environmental conditions acting on macro-scale (e.g. continental-scale climatic conditions) are supposed to set a frame of potential areas suitable for species occurrence from a physiological perspective (fundamental niche) whereas biotic processes (as an integral component of the realized niche) acting on smaller scales select subsets from these areas, where the species actually occurs by accounting for co-occurring species (Soberón 2007). In accordance with this theoretical assumptions, regional-scale limits of species spatial occurrence are shown in various studies to be driven by biotic interactions, whereas abiotic factors (e.g. climatic conditions) are shown to limit species distribution on large spatial scales (Wiens 2011 and references therein).

Besides the hierarchical structure of species niche, scale-dependence of environmental noise has to be named as a second factor influencing the scale-dependence of species distribution patterns. Ecological patterns emerging on small spatial and / or temporal scale are characterised by high levels of uncertainty (e.g. spatial variability of species abundances), which are related to the strong influence of stochasticity on these small scales. In consequence, these high levels of uncertainty impede the interpretation of small-scale patterns (Wiens 1989; Storch et al. 2002). As the scale of resolution increases (gets coarser), local heterogeneity is increasingly averaged out, which makes large-scale ecological patterns more predictable (Wiens 1989).

Both facts, the hierarchical structure of abiotic and biotic processes shaping the realized niche width and distribution of species as well as the scale-dependence of environmental noise are conceptualized in the Eltonian noise hypothesis (Soberón & Nakamura 2009). The key prediction of this hypothesis is that effects of biotic interactions driving species distribution on small spatial scale are averaged out at large scales. In other words, biotic processes shaping small-scale species distribution patterns but are varying across larger scales are dissipating on large spatial scale into statistical noise irrelevant in explaining large-scale species distribution patterns, which are then mainly driven by abiotic environmental conditions like continental-scale precipitation or temperature regime.

Nevertheless, abiotic and biotic processes shaping the species niche space and distribution on local scale are influenced by macro-scale environmental variables to different degrees (Fraterrigo et al. 2014 and references therein). Besides biotic interactions such as competition, microclimate is shown in

numerous studies to drive the spatial occurrence of species on small spatial scale (Opedal et al. 2015; Maclean et al. 2015). The degree to which microclimatic conditions deviate from the surrounding macroclimatic conditions thereby depends on modulating factors acting on local scale. These modulating factors affecting the cross-scale link between micro- and macro environmental conditions can either be abiotic such as micro-topography (Austin & Van Niel 2011; Opedal et al. 2015) or biotic such as microclimate amelioration by vegetation (De Frenne et al. 2013; Schweiger et al. 2015b).

Based on the theoretical framework of the Eltonian noise hypothesis and the profound empirical knowledge about the effect of micro-environmental conditions on species distributions, one can infer that a low degree of cross-scale links between environmental conditions driving species distribution from macro to micro scale will result in a high scale-dependence of species realized niche characteristic and, thus, species distribution. In contrast, strong cross-scale links between environmental factors driving species distribution on small spatial scale and abiotic drivers of species distribution on macro-scale will result in high cross-scale similarity of species realized niche characteristics / species distribution patterns. Furthermore, one can assume that low environmental noise at small spatial scale, which is related to the degree of cross-scale links between micro- and macro environmental conditions, will increase the cross-scale similarity of species realized niche characteristics / species distribution patterns.

Although of major importance for global change research and assessment, knowledge about the scale-dependence of species niche characteristics and the potential causes are lacking up to now. In order to test the theoretically based assumptions stated above for the scale-dependence of species niche characteristics, we focus in this study on the scale-dependence of species temperature niche, one of the most important niche dimensions related to climate change. We therefore combined occurrence data of 19 vascular plant species and the related temperature regime examined over seven orders of magnitude with a spatial resolution of centimetres (local scale), several kilometres (regional scale) and several thousand kilometres (continental scale). The species we are focusing on are frequently occurring in Central European spring fens and other semi-aquatic, groundwater-dependent habitats. The temperature regime of these habitats is strongly controlled by the temperature of the feeding groundwater, which reflects the annual mean temperature of the catchment area and is characterized by a low spatial as well as temporal variability compared to the local ambient air temperature. The abiotic drivers of species occurrence acting on local scale are therefore tightly interlinked with the abiotic drivers, which originate from continental-scale climatic processes and affect species spatial occurrence on regional and continental scale. Furthermore, the spatial occurrence of the investigated plant species is significantly affected by groundwater temperature on regional scale (Schweiger & Beierkuhnlein 2014).

Following the theoretical assumptions about the scale-dependence of species niche characteristics paired with empirical knowledge about the low environmental noise on local scale and the high degree of cross-scale links between micro- and macroscale temperature regime characterizing the studied ecosystems, we hypothesize high degrees of cross-scale similarity for the realized temperature niches of the studied species across a wide range of spatial scale.

Methods

To test the cross-scale similarity of species realised temperature niches, we quantified the spatial occurrence of 19 vascular plant species and the related temperature regime at three different spatial scales, ranging from centimetres to several thousands of kilometres. All investigated species frequently occur in Central European spring fens, which were chosen as study system to investigate species niche characteristics on local and regional scale. Information about species niche characteristics on local and regional scale are based on investigations on the species' spatial occurrence as well as water temperature measurements conducted on spring fens in the forested lower mountain ranges of Central Germany (latitude 49.9–50.68 N, longitude 11.2–12.28 E, 410 to 910 m a.s.l., for more details see Schweiger & Beierkuhnlein 2014; Schweiger *et al.* 2015a). All of the investigated spring fens are characterised by water saturated seepage areas which habit the investigated species and are well differentiated from the surrounding forest habitats. As the feeding groundwater diffusively seeps out of the ground all over the seepage area, the temperature regime of a particular spring fen, is strongly related to groundwater temperature and is very homogeneous all over the site.

Local patterns of species occurrence and the related temperature regime were investigated for 15 spring fens, which is a representative subset of 102 spring fens used for the regional scale investigations. Small-scale patterns of species occurrence and water temperature were investigated for each of the 15 spring fens with a below-metre spatial resolution. Therefore the whole seepage area of each spring fen was sampled in a hexagonal design with an equidistant distribution of plots with 1 m distance between sampling plots. At each sampling plot, occurring plant species were recorded in a radius of 28 cm around the plot centre (equals 0.25 m^2). Additionally, water temperature was recorded in the rhizosphere zone at the centre of each plot. In total, information about species presence / absence and corresponding water temperature was available for 700 sampling plots from the 15 spring fens to model species realised temperature niches on local scale.

Regional-scale niche characteristics were derived from investigations of species occurrence and water temperature regime collected for the 102 spring fens, which are regularly distributed at the landscape scale over a total spatial extent of 2000 km². Species presence/absence of the plant species as well as water temperature were investigated between July and August of multiple years between 1989 and 2013 (1989, 1996, 2003, 2004, 2005, 2013). This resulted in 413 records of species presence / absence and corresponding water temperature used for modelling species realised temperature niches at regional scale. Whereas presence / absence of the plant species was investigated for the whole seepage area of each spring fen, water temperature was measured at the uppermost point within the seepage area, where upwelling groundwater appeared at the surface (for more details see Schweiger et al. 2015a). Niche characteristics on continental scale were derived from combining information from digitalised ranges maps of the species (Altas Florae Europeae, Kurtto *et al.* 2013) with gridded information about mean annual temperature with a spatial resolution of 10 arc minutes (approximately 20 km, Worldclim dataset, Hijmans *et al.* 2005) for whole Europe (approximately 10.2 million km²).

Species realised temperature niches were modelled for each spatial scale based on the corresponding data for species occurrence and temperature regime. We therefore used the classical

Huisman-Olff-Fresco modelling approach (Huisman *et al.* 1993), extended by two binomial model types as well as an improved model optimisation process and model stability check based on bootstrapping (*eHOF*-r package version 1.4, Jansen & Oksanen 2013). In this approach of hierarchical logistic regression modelling, the best model out of seven predefined model types is chosen by balancing the predictive power of the model with its mathematical simplicity (Jansen & Oksanen 2013). The seven predefined response model types, which were all modifications of the logistic Gaussian equation, included one no-response model, two monotonous increasing or decreasing models (linear and plateau-shaped), two unimodal models (symmetric and asymmetric) and two bimodal model types (with equal or unequal maxima). By maximizing predictive efficiency under most parsimonious conditions, HOF models have shown by several studies to be among the best statistical tools to model responses of species occurrence along environmental gradients (Oksanen & Minchin 2002; Jansen & Oksanen 2013).

Based on the modelled response of species occurrence along the gradient of temperature for the three different scales, we used different niche characteristics for cross-scale comparisons. Besides the actual shape of the species-specific response curve, we extracted the maximum probability of occurrence (maximum of response curve) as well as the optimum temperature (temperature for the maximum probability of occurrence) for each species at each scale.

To compare niche characteristics within and among species between the three different levels of spatial scale, we used parametric *ANOVAs (one-factorial and mixed effect models) and* non-parametric, rank-based correlation analyses (Spearman rank correlation). We chose non-parametric correlation analyses as spatial scale was represented as ordinal categories in our study (local, regional, and continental) and sample size of the species we compared across these scale was relatively low (n=19). Rank-based, non-parametric correlation analyses are more robust against these restrictions in data quality than parametric correlation analyses such as Pearson product-moment correlation. Furthermore, rank-based correlation tests assume monotonic relationship but make no assumptions about the actual shape of the relation (e.g. linear vs. non-linear) like parametric tests do. However, non-parametric tests are statistically less powerful than parametric tests, which increases the risk of type I or type II errors especially for small sample sizes like in our case (c.f. Mumby 2002). To overcome this problem we used a Monte Carlo resampling approach by applying an Approximative Spearman Correlation Test ('spearman_test' – command) implemented in the *coin* R packages (v. Hothorn *et al.* 2008) with 9999 resamples. Obtained z-scores were then transformed into correlation coefficients by using the inverse of Fisher z- transformation.

Cross-scale similarity of species optimum temperatures were tested with robust linear mixed effect models by accounting for species identity as random effect ('lmer' – command from the lmerTest package, v. 2.0-29, Kuznetsova *et al.* 2015). We furthermore calculated the cross-scale differences of optimum temperature for each species and each combination of scales and tested these differences with a simple one-way ANOVA. Within species (intra-specific) differences in the niche characteristics between the different scales were calculated by subtracting the species-specific niche characteristic of the next higher scale from the lower scale (e.g. temperature optimum of species i at local scale - temperature optimum of species i at regional scale). To quantify inter-specific differences in the niche characteristics at

a particular scale, we calculated the difference of a particular niche characteristic (e.g. maximum probability of occurrence) of each species from the corresponding niche characteristics obtained for all other species at the same level of spatial scale. All analyses were performed in the R-environment (version 3.2.2, R Core Team 2015) with a level of significance of alpha = 0.05.

Results

We observed high cross-scale similarity of temperature niche characteristics for all investigated plant species across the seven orders of magnitude of spatial scale. For species with uni- and bimodal temperature response curves, temperature optima, meaning the temperature where the probability of occurrence maximises, were similar across the three levels of investigated spatial scale (exemplified for four species in Fig. 1, for all other species see Fig. S1, Supporting material).

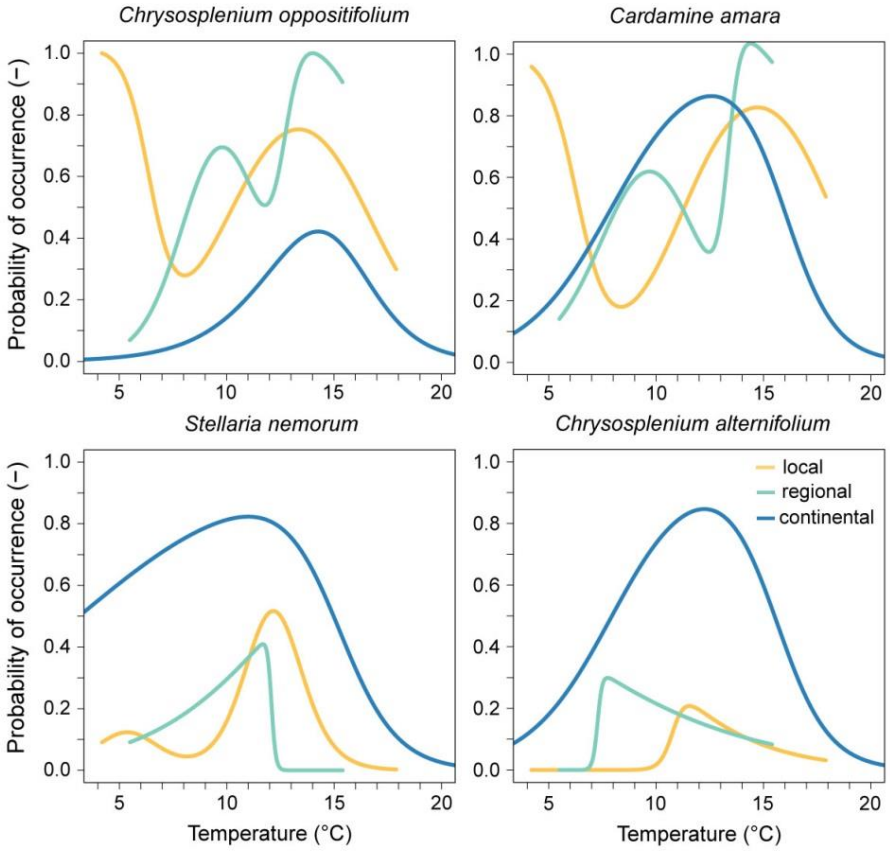

Figure 1: Cross-scale similarity of realised temperature niches of vascular plant species adapted to groundwater-fed wetland ecosystems (spring fens). The investigated spatial scales include the local scale (resolution of 1 m with an extent of several metres, orange lines), the regional scale (extent of 2000 km², green lines) and the continental scale which cover a range of several thousands of kilometres (blue lines). The niche characteristics across the examined spatial scales are exemplified for four of the 19 investigated vascular plant species (see Fig. S1, Supporting information for all other species).

Temperature optima did not significantly differ between the three levels of spatial scale (t = -0.077, df=51, p=0.93 for mixed effect model testing species temperature optima by accounting for species identity and F=0.39, df=2, p=0.54 for the one-way ANOVA testing the calculated cross-scale differences; Fig. 2a).

However, the maximum probability of occurrence significantly increased from local to continental scale (Spearman's rho=0.99 (z= 4.03), p<0.001, Fig. 2b). In other words, temperature as an abiotic /climatic driver explained the spatial occurrence of the investigated species significantly better on continental scale with coarse resolution than on local scale with a fine resolution of species occurrence. Furthermore, the difference in maximum probability significantly increased with increasing spatial scale (see Fig. 2c, Spearman's rho=0.99 (z= 3.08), p=0.0014). Thus, cross-scale differences in the effect size of temperature as driver of species occurrence increased not linearly with scale but are characterised by high non-linearity.

Differences in niche characteristics observed between the different species at one scale significantly decreased with increasing spatial scale. Species-specific differences in temperature optima significantly decreased from 4.7 ± 1.5 °C on local scale to 2.8 ± 0.9 °C on local scale and 2.3 ± 0.6 °C on continental scale (Spearman's rho = -0.99 (z= -5.29), p < 0.001, Fig. 3a). Also inter-specific differences in maximum probability of occurrence significantly decreased with increasing spatial scale (0.37 ± 0.12 °C, 0.34 ± 0.07 °C and 0.17 ± 0.08 °C on local, regional and continental scale, respectively, Spearman's rho = -0.99 (z=-4.86), p < 0.001, Fig. 3b). Cross-scale changes of niche characteristics across the three spatial scales were very similar among the tested species (Fig S2a and b in the Supporting material for optimum temperature and maximum probability of occurrence, respectively).

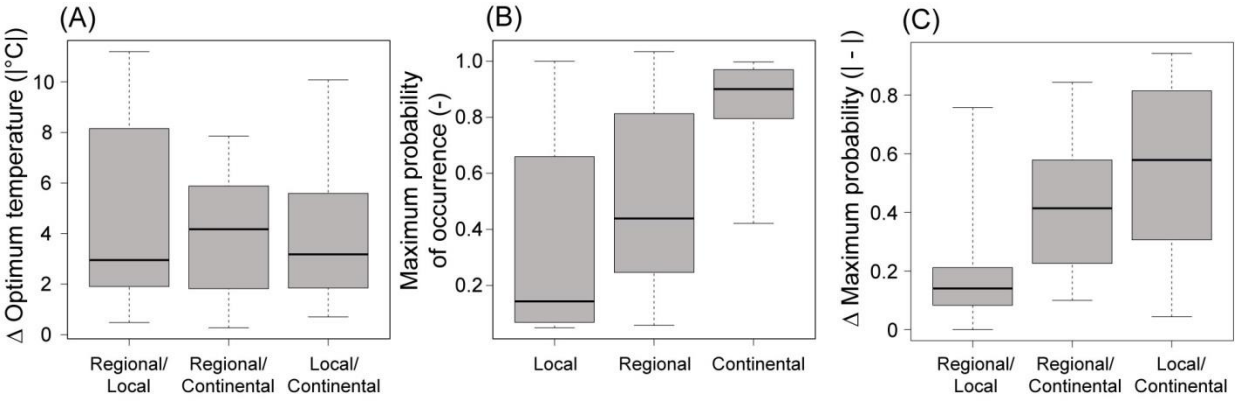

Figure 2: Differences in species-specific niche characteristics across the three investigated spatial scales (n = 19 species). A) Cross-scale differences in species-specific optimum temperatures (temperature with maximum probability of occurrence), B) Species-specific maximum probability of occurrence, C) Cross-scale differences in species-specific maximum probability of occurrence. Differences in niche characteristics (A and C) are expressed as absolute values of the differences.

Overall, the majority of species showed unimodal temperature response curves on local and continental scale (47.4% and 78.9%, respectively), whereas the portion of species with unimodal response curves dropped to 26.3% on regional scale. The portion of species with monotonous temperature response curve was higher at regional scale (26.3%) than at local and continental scale (5.3% and 0%, respectively). Bi-modal response curves were observed for 36.8% of the species on local and regional scale and 21.1% on continental scale. For 10.5% of the investigated species we observed no response to the temperature range examined on local and regional scale, whereas the portion of species with which showed no response dropped to zero on continental scale.

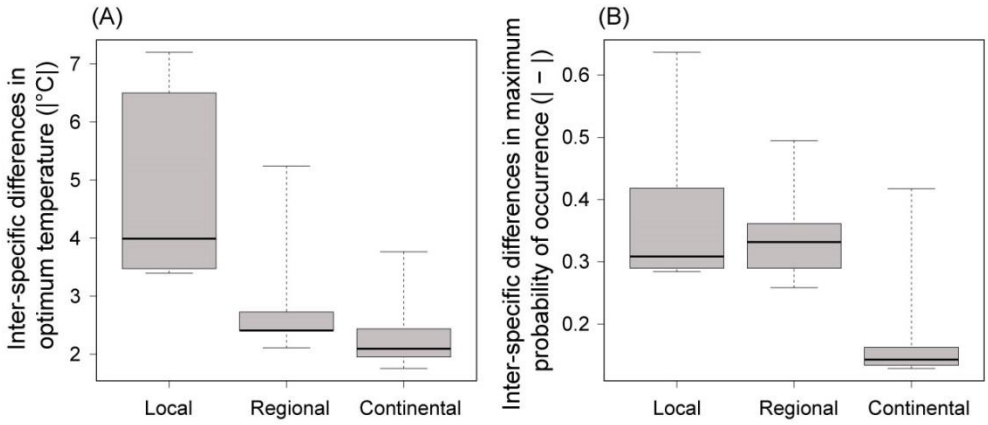

Figure 3: Differences in species-specific niche characteristics within the three investigated spatial scales. A) Differences in optimum temperature (temperature with maximum probability of occurrence) between the investigated vascular plant species (n=19) on local, regional and continental scale, B) Between-species differences in maximum probability of occurrence. Differences in niche characteristics are expressed as absolute values of the differences.

Discussion

The key to understand scale-dependence in complex adaptive systems like ecosystems is to determine fundamental processes (ecological properties) that are maintained when moving across the scales of inquiry (Levin 1999; Whittaker et al. 2001; Peters et al. 2004). High confidence exists about the cross-scale relevance of these fundamental processes in shaping species distribution patterns across a wide range of spatial and temporal scales (Levin 1992). The spatial occurrence and aggregation of species is mainly determined by the species' physiological characteristics, population dynamics and dispersal ability as well as the species interaction with particular environments varying in space and time (Storch *et al.* 2008). The effect of scale is therefore a prerequisite that has to be considered in ecological studies in order to understand the past, the current and potential future patterns of species distribution and, thus, potential future threats to global biodiversity (Hortal et al. 2010). A wide range of spatial or temporal scales has to be considered to gain a more general understanding of species environmental requirements and, thus, habitat selection and distribution patterns (Bowyer & Kie 2006). However, high scale-dependence of

ecological patterns like species-richness patterns as well as strong inter-specific differences in the scale-dependence of environmental drivers diminished the belief in cross-scale universal regulations in ecological systems (e.g. Storch *et al.* 2002; Rahbek 2005; Belmaker & Jetz 2011). Here we observe high cross-scale similarity of species temperature niche characteristics, one of the most fundamental ecological properties related to climate change. This was confirmed for fundamental niche characteristics like the species' temperature optima which were statistically not discriminable between three different spatial scales ranging from a few centimetres to several thousand kilometres.

Understanding when the realized niche characteristics of a species remain similar across scales is important as this is a basic assumption of species distribution modelling which is still strongly debated (c.f. Potter et al. 2013). Several studies report the environmental drivers of plant species spatial occurrences and, thus, niche characteristics to show strong scale-dependence as well as strong species-specific differences (e.g. Crawley & Harral 2001). In contrast, we find similar niche behaviour at different spatial scales based on plot-based species presence vs. rasterised species range maps, measured groundwater temperature vs. interpolated annual mean temperature. As major portions of the tested species showed uni- or bi-modal temperature response curves with temperature optima within the range of examined temperatures, we apparently captured the full temperature niche for a majority of species on all scales. Both facts, the high cross-scale similarity of species niche characteristics as well as the high portion of species with uni- or bi-modal temperature response curves can be explained by the high thermal constancy of the investigated habitats on local and regional scale. Furthermore, the tight cross-scale link between the temperature regimes acting on the different scales of inquiry seems to play a significant role. Both environmental circumstances, low environmental noise on local scale and a strong cross-scale link between micro- and macroclimatic conditions, makes the studied systems quite distinct from the majority of terrestrial ecosystems, where microclimatic conditions strongly varies across larger scales and are quite disjunct from the surrounding macro-climatic conditions (Austin & Van Niel 2011; De Frenne et al. 2013; Opedal et al. 2015, Schweiger et al. 2015b). In many cases it is very difficult or even impossible to detect the signal of species niches, when high amounts of stochastic processes (environmental noise) emerging from different environmental factors (environmental noise) blur the underlying, focal signal / pattern (Palmer & Dixon 1990; Chase & Myers 2011). Spring habitats as well as other groundwater-dependent habitats are characterised by high thermal constancy over long temporal and on landscape scales. This outstanding environmental feature gave us the opportunity to study species responses to an environmental factor without a lot of noise in this driver, which is normally the case on local and regional scale. Furthermore, a tight link exist between the temperature of groundwater, which is strongly affecting species occurrence on local to regional scale (Schweiger & Beierkuhnlein 2014) and the annual mean temperature of a given region affecting species occurrence on continental scale (Simova *et al.* 2011). Thus, the temperature regime acting on local scale in our study systems is tightly linked to the temperature regime on regional and even continental scale. Both facts, the high thermal constancy, thus, low environmental noise as well as the pronounced cross-scale link of the major environmental drivers are rather uncommon for most terrestrial ecosystems but can explain the high cross-scale similarity in species temperature niche characteristics we find in this study. Thus, the inability to detect cross-scale similarity of ecological patterns reported from other studies might be mainly caused by strong effects of

environmental noise characterising ecological systems at small spatial and temporal scales, which is related to loose cross-scale links between micro- and macro environmental conditions (c.f. Wiens 1989).

However, the importance of temperature as abiotic driver significantly decreased with decreasing scale as the species maximum probability of occurrence explained by temperature decreased from continental to local scale. Thus, species spatial occurrence reflected in the examined characteristics of species realised niches seems to be more affected by additional factors besides temperature on small spatial (local) scale than on continental scale. Generally, ecological processes and patterns on small spatial and temporal scale are assumed to be mainly driven by biotic factors related to physiology and morphology whereas patterns and processes occurring on large spatial scale of several hundreds of kilometres or over long temporal periods are mainly driven by abiotic factors related to climate or geomorphology (Holling 1992; Peterson *et al.* 1998; Belmaker & Jetz 2011). Such kind of additional, probably biotic factors acting on small scale seems to be also relevant in our study although temperature turned out to be an important factor similarly affecting species niche characteristics across a wide range of spatial scales. Furthermore, we observed the importance of temperature to increase non-linearly with increasing spatial scale. Both results emphasise, that up- or downscaling of niche-based species distribution models obtained on a certain scale does not follow simple linear rules (c.f. Pearson & Dawson 2003; Peters *et al.* 2004; Belmaker & Jetz 2011).

Besides the scale-dependent importance of biotic and abiotic drivers, scale-dependence of ecological patterns and processes like species richness and species turnover has been shown to strongly differ between species (e.g. Lenoir *et al.* 2012). The detected species-specific differences in niche characteristics in this study strongly decreased with increasing spatial scale. Furthermore, changes in the examined niche characteristics (temperature optimum and maximum probability of occurrence) across the spatial scale under investigation were very similar among the tested plant species. Although, the cross-scale similarity in species niche characteristics differs to some extent for the species we investigated in our study, the realised temperature niche appears to be very conservative and robust across a wide range of spatial scales.

However, cross-scale similarity in ecological patterns and processes is always restricted to a certain range of scales (Kenkel & Walker 1993). This is definitely true for our study as well. The high cross-scale similarity we observe for the realised temperature niche of vascular plant species covers nevertheless the most relevant scales for ecological studies on species distribution patterns. Our results give therefore strong evidence for the idea that a small set of key regulating factors control ecosystem functioning and, thus, services provisioning over a multitude of scales (c.f. Holling 1992).

Although the theoretical concepts, data and analyses seems to be quite simple, the implications of our study are far reaching especially for niche based modelling of species distribution patterns, one of the major tools to assess future effects of climate change on global biodiversity. However, the semi-aquatic ecosystems investigated in this study are quite outstanding in their environmental features. This prohibits a direct generalization of our findings for other terrestrial ecosystems, which are characterized by high levels of environmental noise on small spatial scale. By reporting a high cross-scale similarity of realised

niche for species inhabiting ecosystems where small-scale environmental noise is low and cross-scale links between micro- and macroclimatic conditions are strong, our results can nevertheless help to develop a more general theory about fundamental ecological habits regulating ecological patterns and processes across a multitude of spatial scales.

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Biosketch

Andreas H. Schweiger is a research associate at the Chair of Biogeography, University of Bayreuth with a rather broad focus on ecological and biogeographical processes and patterns on different temporal and spatial scales. Carl Beierkuhnlein is the head of the Chair of Biogeography. He is speaker of the Global Change Ecology study program at the University of Bayreuth. His research interests are ranging from biodiversity research to the ecological impacts of climate change.

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Supporting information

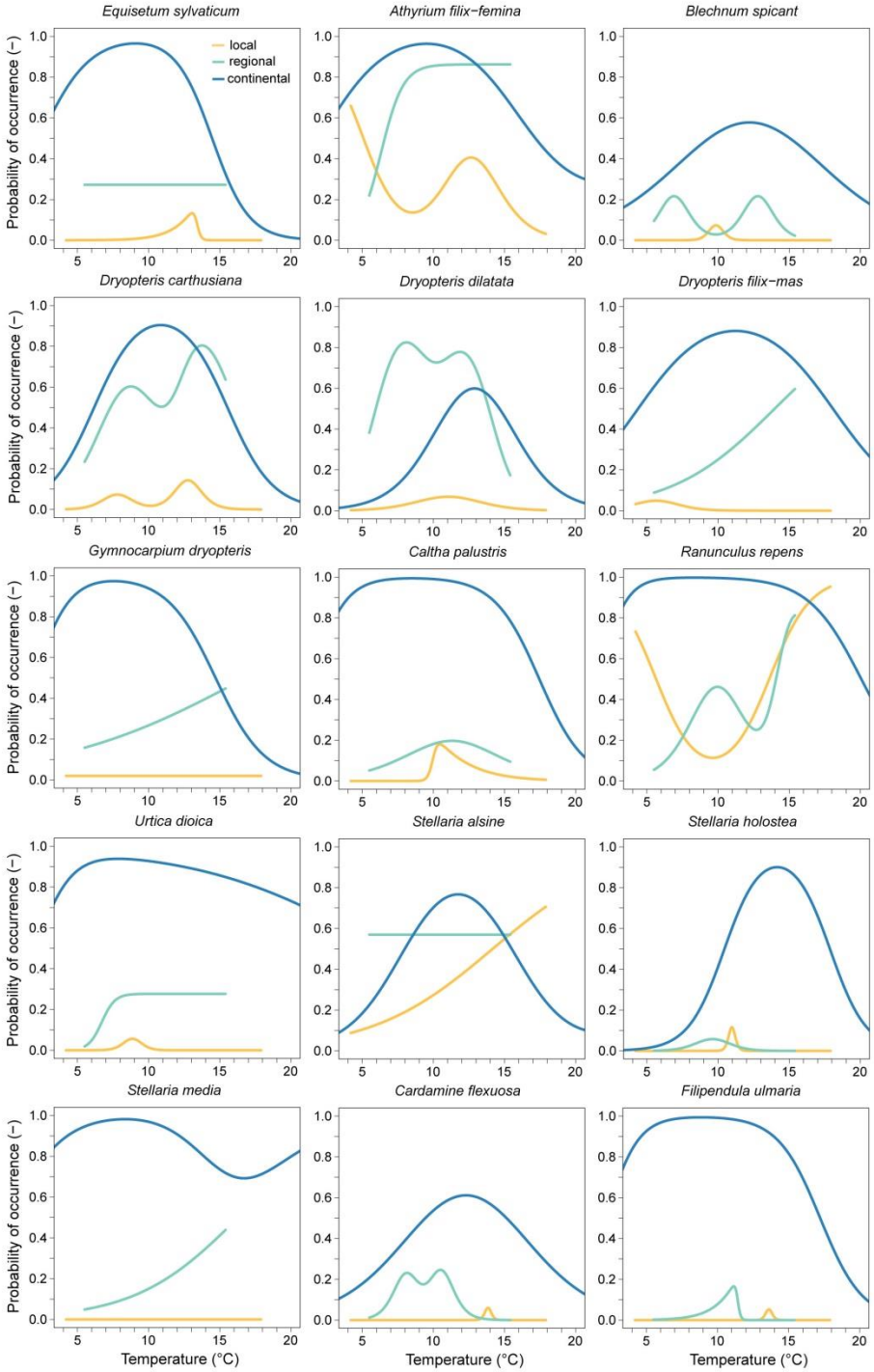

Figure S1: Cross-scale similarity of realized temperature niches of vascular plant species adapted to groundwater-fed wetland ecosystems (spring fens). The investigated spatial scales include the local scale (resolution of 1 m with an extent of several metres, orange lines), the regional scale (extent of 2000 km², green lines) and the continental scale which cover a range of several thousands of kilometres (blue lines).

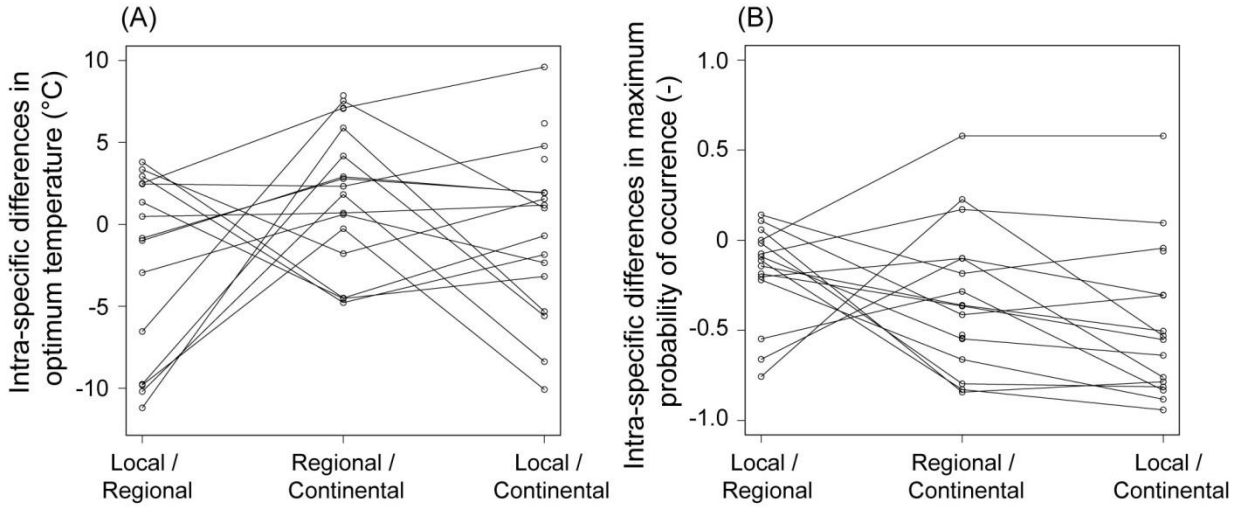

Figure S2: Within-species differences of niche characteristics across the three investigated spatial scales. The within-species differences of optimum temperature (A) and maximum probability of occurrence between the three different spatial scales are depicted for each species separately (n=19) as differences between the particular niche characteristic examined for the different levels of spatial scale.

5.6 Manuscript 6

Optimizing sampling approaches along ecological gradients

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Summary

1. Natural scientists and especially ecologists use manipulative experiments or field observations along gradients to differentiate patterns driven by processes from those caused by random noise. A well-conceived sampling design is essential for identifying, analysing and reporting underlying patterns in a statistically solid and reproducible manner, given the normal restrictions in labour, time and money. However, a technical guideline about an adequate sampling design to maximize prediction success under restricted resources is lacking. This study aims at developing such a solid and reproducible guideline for sampling along gradients in all fields of ecology and science in general.

2. We conducted simulations with artificial data for five common response types known in ecology, each represented by a simple function (no response, linear, exponential, symmetric unimodal and asymmetric unimodal). In the simulations, we accounted for different levels of random and systematic error, the two sources of noise in ecological data. We quantified prediction success for varying total sample size, number of locations sampled along a spatial/temporal gradient and number of replicates per sampled location.

3. The number of replicates becomes more important with increasing random error, whereas replicates become less relevant for a systematic error bigger than 20% of total variation. Thus, if high levels of systematic error are indicated or expected (e.g. in field studies with spatial autocorrelation, unaccountable additional environmental drivers or population clustering), continuous sampling with little to no replication is recommended. In contrast, sampling designs with replications are recommended in studies that can control for systematic errors. In a setting that is characteristic for ecological experiments and field studies strictly controlling for undeterminable systematic error (random error ≥10% and systematic error ≤10% of total variation), prediction success was best for an intermediate number of sampled locations along the gradient (10–15) and a low number of replicates per location (3).

4. Our findings from reproducible, statistical simulations will help design appropriate and efficient sampling approaches and avoid erroneous conclusions based on studies with flawed sampling design, which is currently one of the main targets of public criticism against science.

Key-words

ANOVA, curve fitting, ecological experiment, experimental design, model selection, regression analysis, replication, sampling design, simulation

Introduction

Temporal and spatial gradients are an intriguing and common feature in nature as already realized by the Greek philosopher Heraclites in 500 B.C. and expressed by Plato as '*panta rhei*' (everything flows) (Diels 1895). Major advances in the understanding of our current world have been made through analysing gradients. This is true for all disciplines of science but especially for ecology where, for decades, scientists have dealt with biotic responses along environmental gradients (Ramenskij 1918; Gleason 1939; Curtis & McIntosh 1951; Whittaker 1967; Palmer & White 1994; Sanders & Rahbek 2012).

Numerous concepts in ecology are based on continuous changes of biotic features along abiotic environmental gradients such as the niche concept (Grinnell 1917), coenoclines (Gauch & Whittaker 1972), the intermediate disturbance hypothesis (Connell 1978) or the stress-gradient hypothesis (Bertness & Callaway 1994). Efforts were made in the last decades to develop and test analytical techniques for characterizing single species and whole community responses along environmental gradients in a sound and reproducible manner.

These analytical approaches include the establishment of similarity indices (e.g. Bray & Curtis 1957), univariate regression and multivariate ordination methods (Whittaker 1967; ter Braak & Prentice 1988) as well as the methodological concepts of beta-diversity (Whittaker 1972) and species response curves (Austin 1987; Huisman, Olff & Fresco 1993). Numerous studies exist on how to distribute samples through space and time to optimal cover the underlying ecosystem's variability (e.g. Gillison 1984; Legendre *et al.* 1989; Stein & Ettema 2003). Important methodological concepts like the response surface methodology (Box & Wilson 1951) evolved from the need to increase the prediction success of gradient patterns in natural science (Myers, Khuri & Carter 1989).

Based on the gathered knowledge from all this original research, numerous text books give recommendations about how to plan and conduct ecological sampling and how to analyse the sampled data in order to approximate the underlying pattern as close as possible (e.g. Cochran & Cox 1957; Gregoire & Valentine 2007; Lohr 2009; Gotelli & Ellison 2013). However, a clear guideline about how many samples are needed in which intensity along a gradient under study to most efficiently and accurately identify ecological patterns along the studied gradient is still missing.

Several authors already provide technical assistance to improve sampling with the aim to increase the reliability of results obtained from the sampled data. Adequate total sample size can be estimated using pre-studies (Eckblad 1991) and/or *a priori* power tests (Bartlett, Kotrlik & Higgins 2001; Ioannidis 2005; Bakker, van Dijk & Wicherts 2012). By contrast, for estimating the number of necessary replicates, only approximations based on empirical observations, such as the 'rule of ten' by Gotelli & Ellison (2013), are available. This rule of thumb suggests a minimum number of ten observations per sampling point. However, the authors themselves note that '[…] *the rule of ten is not based on any theoretical principle of experimental design or statistical analysis, but is a reflection of our hard-won field experience with designs that have been successful and those that have not*'. Even less is known when it comes to balancing the number of replications per point of observation against the number of observation points along a spatial or temporal gradient of interest although this is a major source of error in designing ecological

studies (Hurlbert 1984; Quinn & Keough 2002). Based on this lack of information, there are calls for a clear, empirically based guideline about how to optimize ecological sampling (e.g. Bartlett, Kotrlik & Higgins 2001) in order to conduct cost-efficient but still statistically sound analyses. This is especially important as sampling is cost-, time- and/or labour-intensive and, thus, strongly restricted by limited funding which is characteristic for almost every scientific study.

The two main characteristics in sampling design are total sample size and the number of replicates per sampling point along the gradient under study (Gotelli & Ellison 2013). The necessity to take an adequate total number of samples results from the fact that the reliability of findings depends on the total sample size in relation to the random variation that can mask the focal pattern (Eckblad 1991; Bartlett, Kotrlik & Higgins 2001). The replication of observations at each sampled location along a spatial/temporal gradient of a certain environmental factor (e.g. spatial or temporal variation of temperature, pH; hereafter called predictor level) follows two aims: (i) to increase the accuracy of parameter estimation and (ii) to provide information on the natural variation within the data set on which the statistical tests for differences between the predictor levels are applied (Southwood & Henderson 2000; Quinn & Keough 2002). It is obvious that the higher the total sample size and the higher the number of observations per predictor level (n; replicates; for sake of linguistic simplicity, we use replicates for n despite sometimes in the literature it is also applied to $n - 1$), the more precisely one can estimate the underlying pattern. If the number of total observations is constant, there is an inevitable trade-off between the number of observations which can be sampled per predictor level and number of sampled predictor levels along the gradient of interest. Up to now there has been no technical guidance about how to balance the number of predictor levels and the number of replicates when aiming for maximum prediction success under limited resource (i.e. total sample size).

For the study of a response variable along a gradient of a certain predictor, practically any solution ranging from only two predictor levels with many replicates to many predictor levels with no replication can be found in the recent literature (Scheiner & Gurevitch 2001; Quinn & Keough 2002; Gotelli & Ellison 2013). Ecologists are usually interested in differences of biotic response under certain environmental settings (traditionally experimental ecologists) or study the actual shape of a biotic response along the gradient of a certain environmental factor (field- and macro-ecologists). Based on these two different ways of studying ecological response to environmental changes, two major methodological approaches are common in current ecological research. Field- and macro-ecologists tend to sample gradients continuously (in a systematic or preferential manner) but without replication (‘regression approach’: Mac Nally 2000; Quinn & Keough 2002). In contrast, experimental ecologists traditionally use replicated sampling of two to few predefined predictor levels (‘ANOVA approach’: Cottingham, Lennon & Brown 2005; Beier *et al.* 2012). However, also in experimental ecology, recently a call for ‘regression-based experimental design’ has been launched that comes along with reduced replicates but higher numbers of predictor levels (Cottingham, Lennon & Brown 2005; Beier *et al.* 2012; de Boeck *et al.* 2015). However, no feasible methodological recommendation exists for this way of conducting ecological experiments so far.

Under natural, non-experimentally controlled conditions biological systems are characterized by high random variation, which will likely dilute the underlying relationships of interest (Quinn & Keough 2002; Lohr 2009). Furthermore, data from field investigations can be affected by a complex interplay of various interacting or opposing gradients. Such factors can be seen as systematic errors in the biological response along a gradient under study and can hamper the study of responses to one specific environmental gradient (Gauch & Whittaker 1972; Richardson *et al.* 2012; Steinbauer *et al.* 2012). Thus, measurements in natural systems are always subject to errors and uncertainties related to measurement errors, ecological and environmental stochasticity and unaccounted, additional influencing factors (Taylor1991; Clark 2003; Richardson *et al.* 2012).

Using artificial data instead of 'real world' data allow excluding or adding random variation and systematic errors to a known degree to the 'observational' data. In this paper we use simulations based on artificial data with known properties in terms of random and systematic noise to address the problem of how to balance the number of predictor levels sampled along a gradient of a certain environmental factor and number of replicates per predictor level in order to maximize prediction success of the underlying 'true' pattern. By varying random as well as systematic noise in the data, we provide a statistically sound and reproducible guideline about how to optimally sample ecological data, which is applicable in all fields of ecology and science in general.

In our simulations, we assume that a 'true' relationship between gradual changes of an environmental factor and the ecological responses thereon follows a defined response shape that corresponds to a common mathematical relationship. We add random and/or systematic errors of different degrees to the data set, which can mask the 'true' relationship. Then, we draw samples from the simulated gradients by using different sampling approaches and compare the results to the underlying, 'true' pattern.

Materials and methods

MODEL SELECTION AND ARTIFICIAL DATA CONSTRUCTION

We simulated five response shapes frequently occurring in ecological studies (no response as a null model/ control, linear response, exponential decay, unimodal response with centred maximum and unimodal response with non-centred maximum) based on simple linear models (see Table 1; inlets in Appendix S1). The response variable (y) thereby represents any kind of biotic response (e.g. species richness, photosynthetic rate, biomass, phylogenetic diversity) that varies along a gradient of the predictor variable (x), which, in turn, represents any kind of spatial or temporal change of environmental conditions (e.g. spatial/ temporal change of temperature, pH, disturbance intensity). To make our inferences easily transferable to any response and predictor variable independent of the studied system, we scaled our parameters in arbitrary units (predictor variable from 0 to 1000, response variable from 0 to 1).

Table 1. Response shapes considered in the comparison and functions used for their implementation as well as parameterization in the simulations

Response shape	Function	*a*	*b*	*c*	# of parameters
No response	$y = c$			0.5	1
Linear	$y = ax+c$	–0.001		1	2
Exponential decay	$y = \exp(-x^a)$	0.3			1
Unimodal centred	$y = ax^2 + bx$	$-4 \cdot 10^{-6}$	$4 \cdot 10^{-3}$		2
Unimodal non-centred	$y = ax^2 + c$	$-1 \cdot 10^{-6}$		1	2

Data sampled from natural systems always include errors and uncertainty (Taylor 1991). Traditionally, two types of error can be classified depending on their way of affecting the sampled data and, thus, the statistical inference drawn from it (Richardson *et al.* 2012). Whereas the so-called random error combines non-directional noise which influences the response variable in addition to the main predictor in a stochastic and, thus, unpredictable way (observed value = expected value + random noise; Fig. 1a), 'systematic error' summarizes a bias in the data which is constant but unknown (Abernethy, Benedict & Dowdell 1985). This systematic error may originate, for example from spatially clustered environmental characteristics, population effects or any other non-accounted or non-accountable influential factor (observed value = expected value + random noise + systematic influence; Fig. 1b).

In order to reflect different levels of random variation in the simulated data, we assumed that the observed values of the response variable are scattered around the expectancy value of a certain predictor level with a normal distribution that corresponds to a standard deviation (*sd*) of 0·02, 0·05, 0·1, 0·15, 0·2 and 0·25 units, that is 2% to 25% of the total variation. Information about the levels of random noise in 'real-world' data is extremely rare, and only very few studies explicitly focus on the quantification of random noise in ecological data. Based on sampling designs to explicitly quantify random noise in eddy flux measurements, a highly uncertain method in environmental science, Richardson *et al.* (2012) estimated random noise to reach a maximum of 23% of total variation. Similar levels of random noise were quantified by Kelly *et al.* (2009) for an ecological quality index for rivers based on the community composition of diatoms where random noise varied between 3 and 22% of total variation (on average 11·3 ± 4·6%). As the levels of random noise observed in both studies are completely covered in our simulations, we believe that our simulations will be of practical use in many 'real-world' situations.

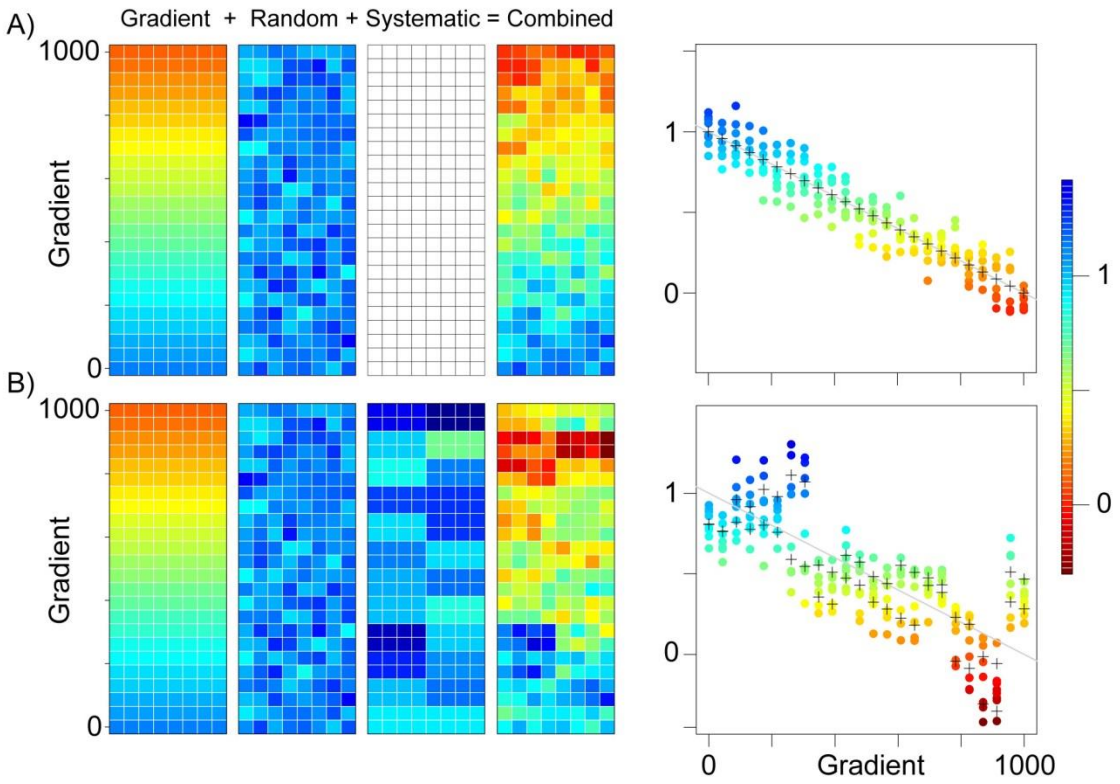

Fig. 1. Artificial data for (a) only random error or (b) random and systematic error. The observed value was combined from the sum of (i) an expected value from a gradient, (ii) a random error (here 10% of gradient length) and (iii) a systematic error (here 20% of gradient length). The eight grid cells per considered predictor level along the gradient (l = 24) represent eight samples (n = 8) considered for each predictor level. In the right panel, the grey trend line indicates the gradient (expected value without errors) and '+' expected values without random error (gradient and systematic error). The points represent the samples drawn at each predictor level along the gradient (equal grid cells of 'Combined').

In addition to the non-directional effect of the random error, we added different levels of systematic error to account for factors, which are not yet covered in the actual study but have a directional effect on the observed response pattern. This systematic bias added to the data can be considered as a 'fully systematic error' (c.f. Richardson *et al.* 2012) as it influences all drawn samples to the same degree. To implement this additional, structured noise in our data, we randomly shifted the 'true' expectancy value y_i independently at each predictor level x_i sampled along the gradient by 0% to 25% of total variation (*sd.err* = 0, 0·02, 0·05, 0·1, 0·15, 0·2 and 0·25 units, respectively). Thus, the extent by which a certain level of systematic error shifted the 'true' expectancy values y_i at a certain predictor level x_i was similar for all simulations but differed in the direction (whether y_i was over- or underestimated) for the different simulation settings (e.g. different response shapes, levels of random variation). Afterwards, we added different levels of random error in addition to the systematic error by sampling normally distributed around the new, shifted expectancy values (again random variation *sd* of 0·02, 0·05, 0·1, 0·15, 0·2 and 0·25 units, respectively, Fig. 1b).

We considered 31 different values for *total number of observations* (*N*) with a minimum sample size of 6 followed by a stepwise increase of total samples size from 10 to 300 in steps of 10 (i.e. N = 6, 10, 20, ..., 300). In combination with the six different levels of random and seven levels of systematic errors, respectively, we tested a total of 1302 combinations of study settings. In agreement with common recommendations in ecological literature about gradient analysis in ecology (e.g. Kenkel, Juhász-Nagy & Podani 1989; Quinn & Keough 2002), we placed the sampled predictor levels evenly (equidistantly) along the gradient of 0–1000, with the two end points always being sampled. The *number of predictor levels* (*l*) ranged from 2 to the total number of observations (*N*). The *number of observations per predictor level* (*n*) varied from one observation (no replication) per predictor level ($n = 1$) to 50% of total number of observations ($n = N/2$). For each value of *N*, all whole-number factorizations $N = n \cdot l$ were considered. For example, if the total number of observations was $N = 6$, we compared three different sampling strategies: 6 predictor levels with 1 observation per level, 3 predictor levels with 2 replicates per level and 2 predictor levels with 3 replicates per level.

EFFECT OF SAMPLING APPROACH ON CORRECT PATTERN IDENTIFICATION

The data set for each parameter combination (response shape × level of random variation × level of systematic error × total number of observations × number of observations per predictor level) was subjected to a simple linear, one-factorial regression analysis between a response variable y (e.g. species richness) and a predictor variable x (e.g. spatial/temporal change of temperature) with the five response shapes (transformations of the predictor x) of Table 1 to choose from by using the *lm*() command in R (v. 3.0.1, R Development Core Team 2013). Replications sampled for the particular predictor levels were thereby treated as independent observations. The most appropriate model among the five options was then selected based on AICc, which takes model complexity and total sample size into account (Burnham & Anderson 2002). For each parameter combination, we repeated sampling and the subsequent analyses 1000 times.

In a next step, the statistically inferred response shape was compared to the 'true' response shape in two ways. In the *correct model* approach, we calculated the fraction of correctly detected response shapes (irrespective of the model parameters). We therefore defined a pattern to be correctly predicted, when the response shape chosen from the algorithm based on AICc was the same as the predefined, 'true' response shape. We calculated the fraction of correctly predicted response shapes for each combination of *N*, *l* (*n*), *sd* and *sd.err* from 1000 model runs.

The *precision of prediction* approach quantified how much the inferred response shape deviated from the actual response shape (irrespective of the function type). For this second approach, we calculated the absolute deviation of the predicted response shape from the 'true' response shape by using a numerical integration approach. Therefore, we summed up the mean absolute differences between the predicted and true response value ($| \hat{y}_i - y_i |$) for a defined number of predictor levels along the gradient under study with $x_i = 0, 10, 20, ..., 1000$ and divided this sum by the number of considered predictor values (101). As a result, the area enclosed between the 'true' and the predicted response shape along the whole gradient

under study standardized by the number of sampled locations along this gradient is calculated. The derived values were then divided by the maximum deviation between inferred and true response pattern, which could be observed among all five response shapes for the respective level of random variation. The complement of these standardized values (i.e. 1 – value) increases with increasing precision towards 1 and was defined as *precision of prediction* (POP).

Besides the type II error (chance of failing to detect a present pattern) which is captured by these first two approaches, we also captured the type I error problematic (chance of detecting a non-existent pattern) in a third approach. Using the no-response pattern as a basis, we calculated the fraction of cases where patterns were erroneously detected from 1000 model runs for each combination of N, l (n), sd and $sd.err$.

To visualize the simulation results, we plotted the fraction of correctly detected response shapes and the POP values for each of the five response shapes as well as a mean of these (excluding the no-response pattern) as a function of the total number of observations, the number of predictor levels and the number of replicates. Trend surfaces for the visualizations were fitted by using least-squares based on a third-order polynomial (*surf.ls*() and *trmat*() commands of the spatial package in R, v. 7.3-7; Venables & Ripley 2002) as well as isolines (*contour*() command implemented in R). The same was done for the fraction of erroneously detected pattern detection based on the no-response pattern.

All simulations and calculations were conducted in R with the add-on packages CATOOLS (v. 1.14, Tuszynski 2012) and AICCMODAVG (v. 1.35, Mazerolle 2013). In order to handle the large computational capacity required to calculate the simulations, the MULTICORE package (v. 0.1-7, Urbanek 2011) was used to run parallel computations of simulations on a multiple core server with a Linux operating system. Statistical relationships were tested with Pearson correlation analyses as well as simple linear models with a level of significance of alpha = 0·05. Visualization was supported by the R packages FIELDS (v. 7.1., Nychka, Furrer & Sain 2014) and CLASSINT (v. 0.1-21., Bivand 2013). The scripts we implemented in R for simulation can be found in the electronic appendix.

Results

The prediction success, expressed as the probability to detect the correct response shape (*correct model* approach) and the precision of this prediction (POP), was strongly related to the number of predictor levels l and the number of replicates per predictor level n (see Fig. 2 as well as Appendix S1). We observed a strong increase in the prediction success from 2 to about 10 predictor levels, almost independent of the total number of observations and the level of random variation. Except for a very low total number of observations below $N = 10$ and the no-response pattern, this was true for all levels of random variation (sd) and all tested response shapes in both approaches (Appendix S1 and S2).

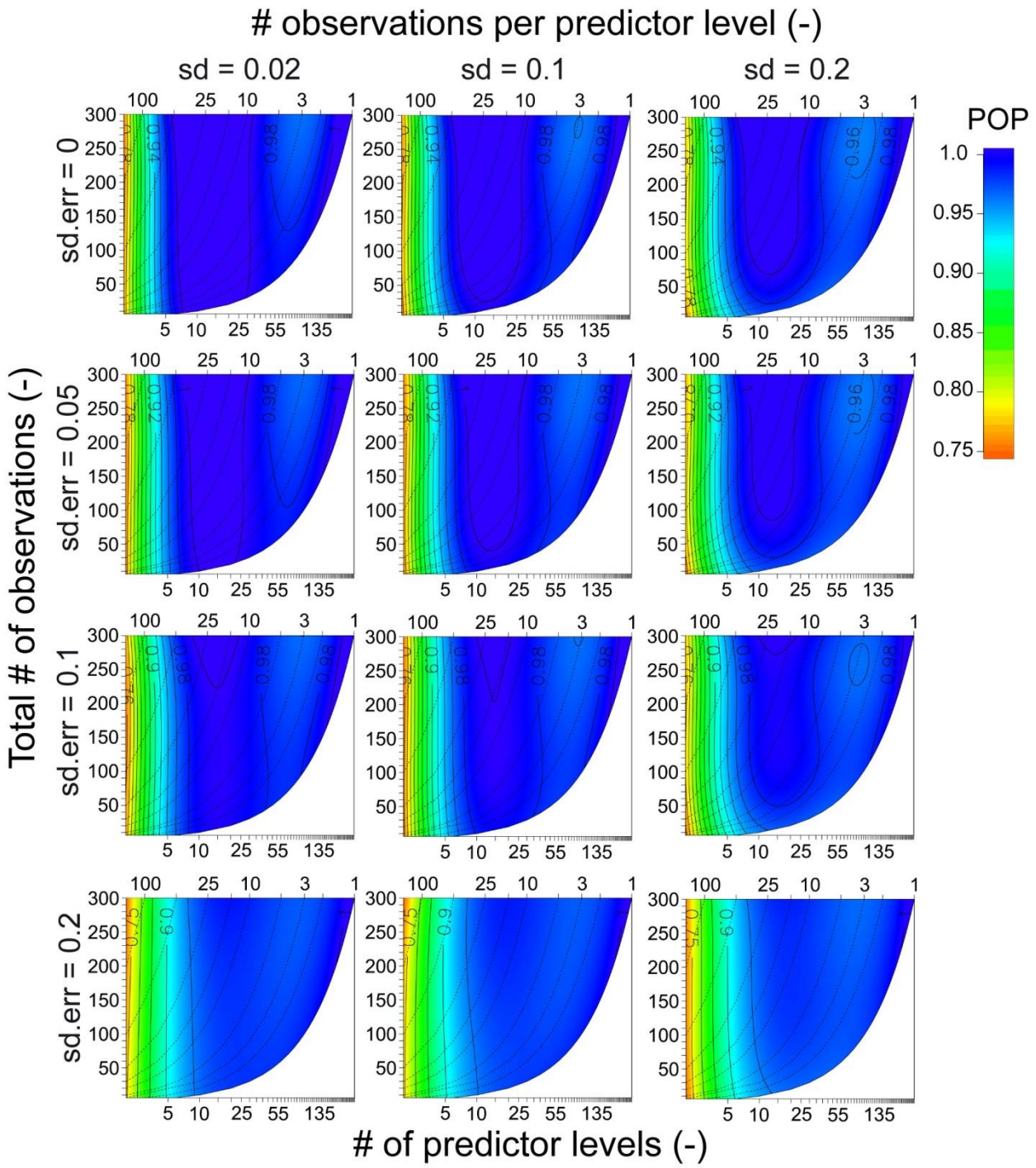

Fig. 2. Prediction success depicted as the precision of prediction (POP) for three different levels of random variation (sd = 2%, 10% and 20% of total variation) and four different levels of systematic error (sd.err = 0%, 5%, 10% and 20% of total variation) based on an average of the tested response patterns (with- out no-response). POP values dependent on the total number of observations, number of predictor levels and number of observations per predictor level are depicted. Solid lines show isolines for a selection of POP values, and dashed lines show isolines for a selection of number of observations per predictor level.

The correct model was detected in more than 90% of cases for all parameter combinations and response shapes within a range of *l* from about 10–30 (for exact values, see Appendix S2a, c, e and S3). We observed this optimal range of number of predictor levels for all levels of random variation (*sd*). The same range of *l* was also true for the precision of prediction approach, in which the POP values reach the maximum of 1 (Appendix S2b, d, f). With further increase of *l*, concomitant with decreasing *n*, however, the probability of correct prediction decreased again. Thus, an intermediate number of predictor levels of *l* = 10–15 turned out to be optimal, regardless of the total number of observations and level of random variation along the sampled gradient. This optimal, intermediate number of predictor levels holds true for low to intermediate levels of systematic errors below 15% of total variation. For a systematic error ≥15%, the adverse effects of a higher number of predictor levels disappeared. For high levels of systematic error, prediction success reached its maximum at $l \geq 10$ and stayed constant with increasing *l*, although overall prediction success was lower for higher levels than for lower levels of systematic error (Fig. 2).

Besides the number of predictor levels, also the number of replicates per predictor level *n* strongly affected the prediction success. Although the overall prediction success decreased with increasing levels of random variation, the need to take replicates in order to maximize prediction success significantly increased with increasing levels of random variation. While no replication was needed to reach the highest possible prediction success for low levels of random variation (*sd* = 0·02 and 0·05), it was indispensable at higher levels of random variation ($sd \geq 0{\cdot}1$, see Appendix S1). Our simulations show that on average *n* = 3 observations per predictor level in combination with *l* = 10–15 predictor levels along the gradient are appropriate to achieve the highest possible prediction success for a systematic error of ≤10% of total variation (see Fig. 2 for *sd.err* = 0–0·1 and *sd* = 0·02, 0·1 and 0·2). For these low to intermediate levels of systematic error, our simulations highlight an increasing need of replicates with increasing random variation to achieve the highest possible prediction success (i.e. POP = 1) with minimum effort (lowest possible *N*). This positive correlation between the level of random variation and the number of necessary replicates was significant under the absence of a systematic error (Pearson's $r = 0{\cdot}98$) as well as for a systematic error of 2% ($r = 0{\cdot}99$) and 5% ($r = 0{\cdot}98$) of total variation ($P < 0{\cdot}001$ and d.f. = 4 in all cases). The positive effect of increasing random variation on the number of necessary replicates increased with increasing systematic error up to 5% of total variation. However, replication was negligible when the systematic error exceeded 10% of total variation.

Regarding type I error problematic (chance of detecting a non-existent pattern), the probability to erroneously detect a pattern strongly increased with increasing systematic error (Appendix S4). Maximum probability for erroneous pattern detection was 30–32% when no systematic error was added to the data but strongly increased for 5% of systematic error. While increasing random error enhanced the probability of erroneous pattern detection under the absence of a systematic error (Appendix S4 for *sd.err* = 0), increasing random error mitigated the effect of an increasing systematic error on erroneous detection probability (Appendix S4 for *sd.err* = 0·05, 0·1 and 0·2). Under the absence of a systematic error (*sd.err* = 0), at least *n* = 2–3 replicates per predictor level were necessary to avoid an erroneous detection of inexistent patterns. This positive effect of taking replicates increased with increasing random error but

strongly decreased with increasing systematic error (*sd.err* ≥ 0·05). Thus, a low to intermediate number of replicates decreased the risk of detecting inexistent patterns but intermediate to high levels of systematic error (≥5% of total variation) diminished this positive effect of replicates and significantly increased the risk of an erroneous detection of non-existent patterns, that is led to an inflation of the type I error.

Discussion

PREDICTION SUCCESS UNDER EXPERIMENTAL SETTINGS VS. FIELD CONDITIONS

Our simulations show that low numbers of predictor levels (points in space/time sampled along spatial/temporal gradients) in combination with medium to high numbers of replicates, that is the typical approach among experimental ecologists, may not be the most effective way to detect response shapes in environmental factors that continuously change along gradients. Our results suggest aiming at increasing the number of predictor levels and, in exchange, reducing but not abandoning replication if total sample size is restricted. In other words, it seems to be more advantageous for experimental ecologist studying gradients to move away from the approaches typically using two to three predictor levels and many replicates.

We recommend a similar sampling approach for field studies, which effectively control for high levels of systematic error by *a priori* excluding or at least minimizing additional interfering variables that might alter the underlying pattern of interest. Sampling a high number of predictor levels along the gradient under investigation with no replication at individual predictor levels, which is widespread among field- and macro-ecologists, may not always be an appropriate solution. Instead an intermediate number of predictor levels in combination with a low number of replicates (10–15 predictor levels and 3 replicates) seem to be in many cases a better road to prediction success when high levels of random variation (in our case ≥5% of total variation) and/or low to intermediate levels of systematic error (≤5% of total variation) can be expected. If, however, higher levels of systematic error are likely (in our case ≥10% of total variation), continuous sampling without replication becomes preferable compared to sampling fewer predictor levels along the gradient with replications. This is especially the case for field studies along gradients that do not explicitly control for additional disturbing factors such as biotic interactions (e.g. competition) which might alter the effect of the underlying abiotic driver of a biotic response (e.g. species occurrence or abundance).

Comparing a set of functions that corresponds to response shapes frequently found in ecology, we showed that an intermediate number of 10–15 predictor levels along the gradient under investigation in combination with three observations per predictor level maximize prediction success for intermediate to high levels of random variation (≥5% of total variation) and small to intermediate levels of systematic error (≤5%). Thus, taking ten replicates per predictor level, as recommended by Gotelli & Ellison (2013), based on field experience will likely cause unnecessary oversampling. This holds true for all response shapes tested in our study: the linear response, the exponential decay and the two unimodal response patterns with centred and shifted maximum.

IMPLICATION FOR FUTURE STUDIES IN ECOLOGY

The preservation of quality in scientific studies is of particular importance as 'unreliable research' is currently one of the main targets of public criticism against science (e.g. The Economist 2013). Several studies conducted in cancer research, neuroscience and psychology, which had high impact on society and economics, recently turned out to lack the required reproducibility (e.g. Prinz, Schlange & Arrowsmith 2011; Simmons, Nelson & Simonsohn 2011; Begley & Ellis 2012; Shanks *et al.* 2013; Open Science Collaboration 2015), a major pillar of science. In most cases, the reason for this was low statistical power of the studies caused by small sample size and/or a small number of replicates (Bakker, van Dijk & Wicherts 2012; Begley & Ellis 2012; Button *et al.* 2013). However, flawed sampling design is not an exception, but seems to be a relatively widespread phenomenon in science (Ioannidis 2005). To counteract this problem, several authors strongly recommend a careful sampling design based on knowledge from previous studies (Legendre *et al.* 1989; Bakker, van Dijk & Wicherts 2012). Ioannidis (2005) suggests a general increase in sampling effort but hints at the same time at the associated rising costs. Our simulations offer a solid basis to further improve experimental and sampling design in ecological studies and, thus, may play an important part in contributing to save funds and labour without an associated loss of quality.

LIMITATIONS OF OUR SIMULATION APPROACH AND OUTLOOK

To maintain the straightforward message of our study, we had to restrict the tested simulation settings to relatively simple functions with only one major gradient (predictor). We assume that this covers the situation in a significant fraction of ecological studies as well as studies from other disciplines. However, the simulation and testing framework presented here could possibly be extended to more complex function types (like breakpoint or sigmoid functions; Matthews *et al.* 2014 or power functions; e.g. Dengler 2009) or to more than one predictor of interest (multifactorial or mixed effect models). The latter is particularly relevant in experimental studies where two or more factors are crossed (factorial design), but also in observational studies where often more than one environmental driver of biotic patterns interact.

Furthermore, we equidistantly placed the predictor levels (sampling locations) along the gradient under study. We, thus, did not consider the effect of preferential sampling along environmental gradients which is, for example applied by the gradient-oriented sampling (gradsect method; Gillison 1984) or the adaptive-sampling approach (Thompson & Seber 1996). As organisms are often not randomly distributed along environmental gradients but lump in preferential ranges (Fortin, Drapeau & Legendre 1989; Legendre *et al.* 1989), future studies should also elaborate on the effect of preferential sampling to further increase sampling efficiency. However, the need of detailed a priori knowledge about the ecological niche characteristics that is still lacking for many organisms may hamper preferential sampling. While all these mentioned topics can be seen as a limitation of the present study, our results provide a first, clear and reproducible guideline about how to optimize sampling along ecological gradients.

Our study did explicitly not implement standard goodness- of-fit approaches (like R^2, or f-statistic based p-values) as these measures are susceptible to systematic errors. Sampled data modified by systematic error might be perfectly predicted by a model, which does not match the 'true' underlying pattern. This is particularly true in scenarios with few predictor levels and many replicates where an erroneous model could still score high R^2 values, leading to entirely wrong conclusions. These erroneous conclusions caused on high values of standard goodness-of-fit approaches stress the importance of approaching scientific questions with consistent theory and quantifying possible sources for systematic errors.

Our simulations show that replication is inevitable in experimental studies and advisable for observational field studies, unless unaccounted systematic errors occur, potentially distorting the underlying pattern. This is especially true, when the random error is high. However, optimal sampling strategies have to be selected context-dependent and differ with the required accuracy, which has to be achieved, as well as the number (uni- or multivariate) and the mathematical character (discrete or continuous variables) of the variables tested in the particular study (Kenkel, Juhász–Nagy & Podani 1989). Although this context-dependency of sampling strategies seems to impede general statements about optimal sampling strategies, a systematic and reproducible approach like ours could help to set clear framework conditions on which future studies could build on in order to further optimize sampling in ecology and possibly also in other scientific disciplines. Based on our results, we infer basic guidelines for gradient sampling in Box 1.

Box 1. Optimal gradient sampling in a nutshell for situations with one major gradient (or one factor to be tested) and when more complex response shapes than those of Table 1 are not expected.

1) In **controlled environments** (i.e. experiment-like settings): Intermediate number of points in space / time sampled along spatial / temporal gradients (10 to 15) and a low number of replicates per point (3), suggests a total sample size of 30 to 45. This approach is also sensible for field ecologists, if confidence is high that a possible systematic error (i.e. unknown additional predictor variables) is controllable.

2) Under **field conditions** (i.e. high levels of systematic error): If systematic errors are unaccountable or are likely to be high, gradual sampling with no replication should be preferred. However, predictor levels and sample size necessary to obtain high prediction success strongly increase with increasing systematic error (in our case on average >200).

3) **Type I error inflation by systematic errors**: The probability of an erroneous detection of a non-existent pattern (type I error) significantly increases with increasing systematic error (bias in the data which is constant but unknown).

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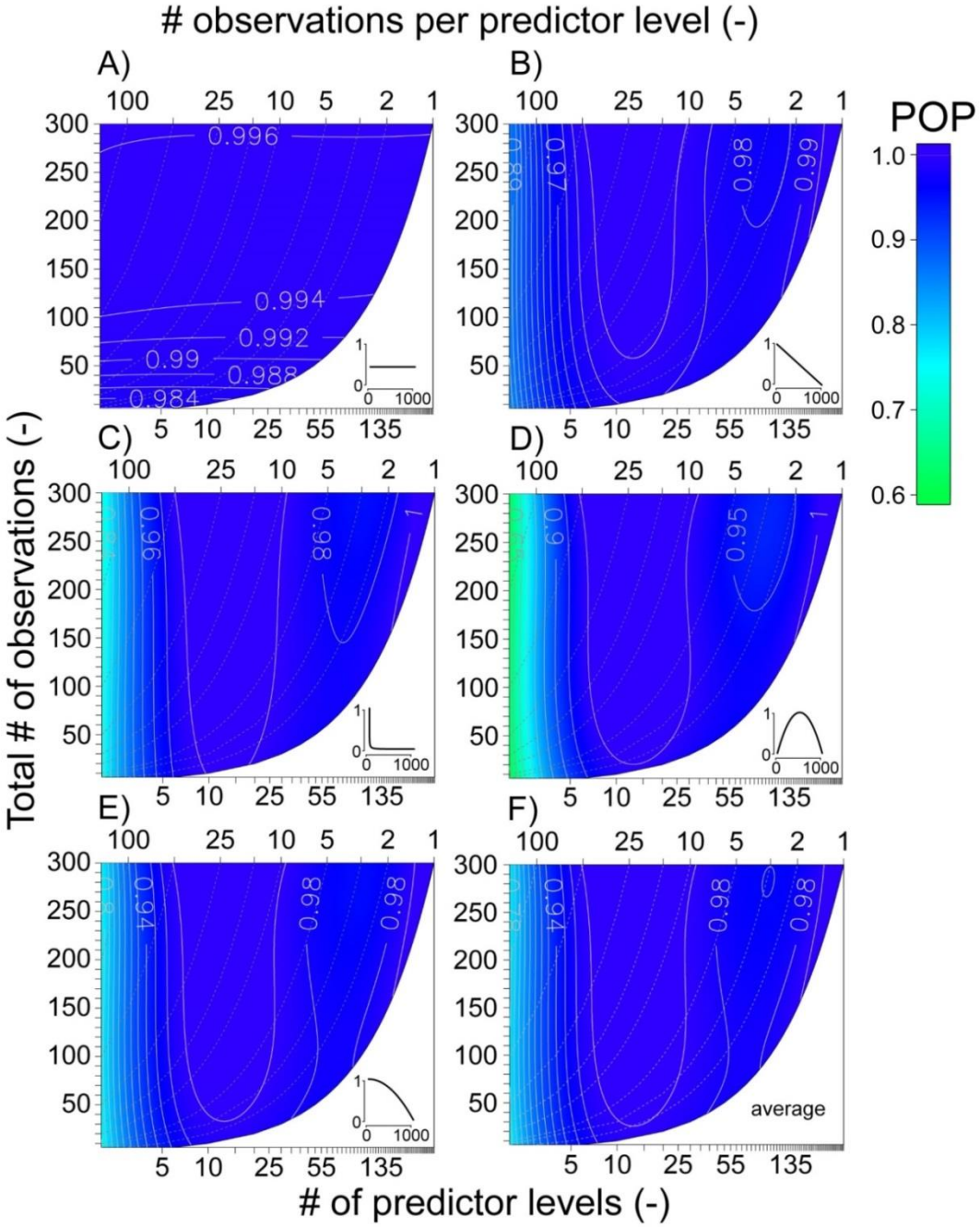
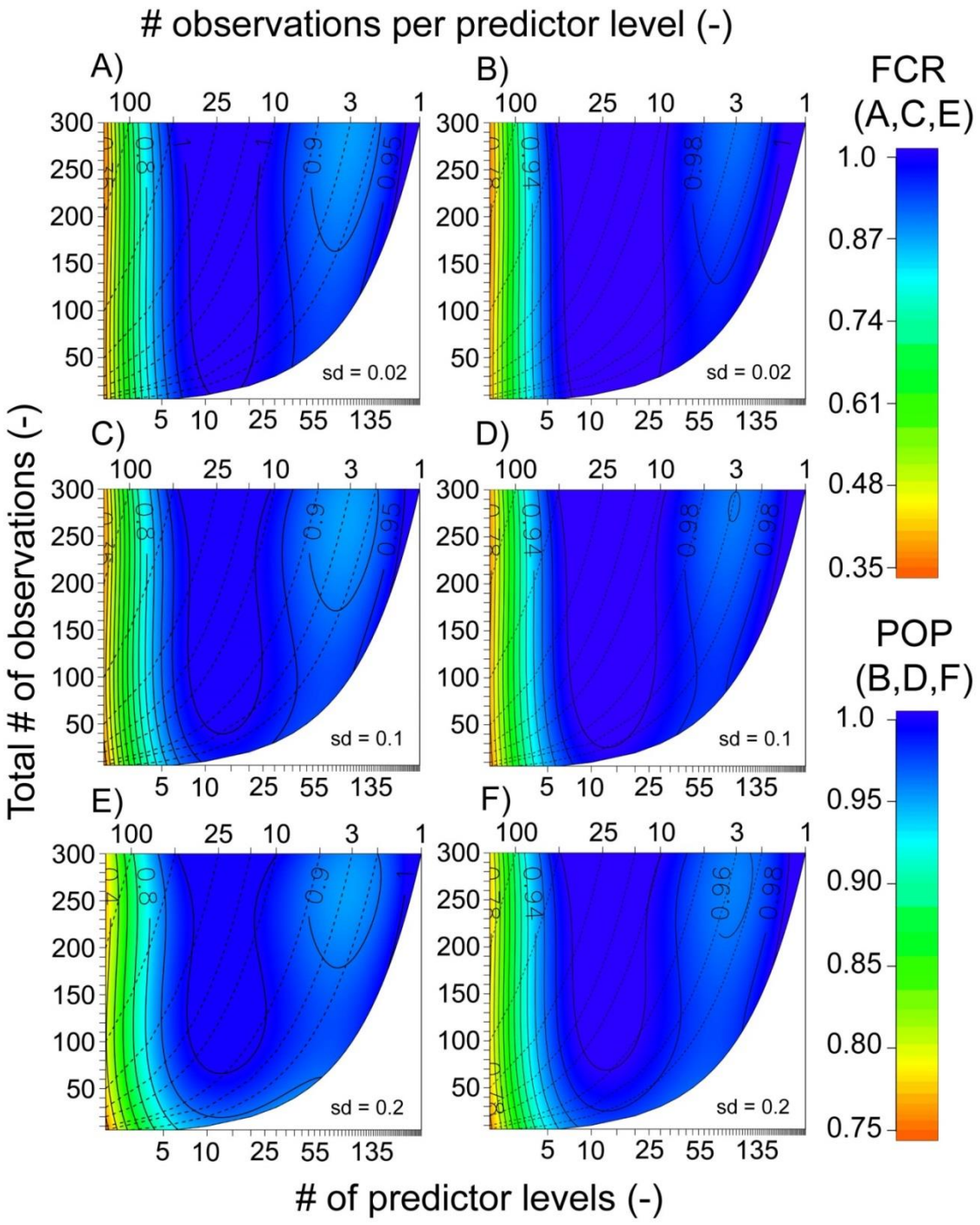
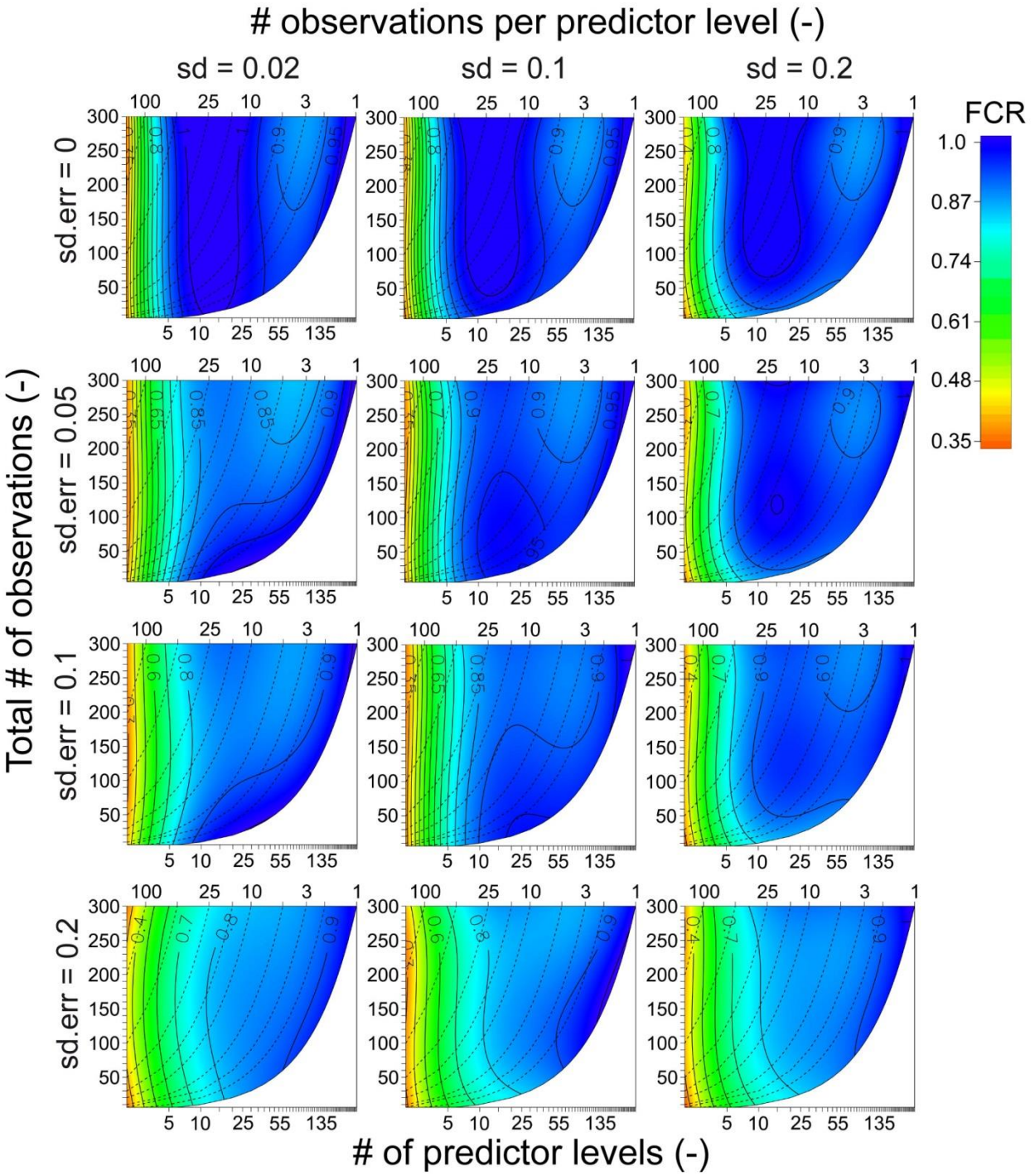
Supporting Information



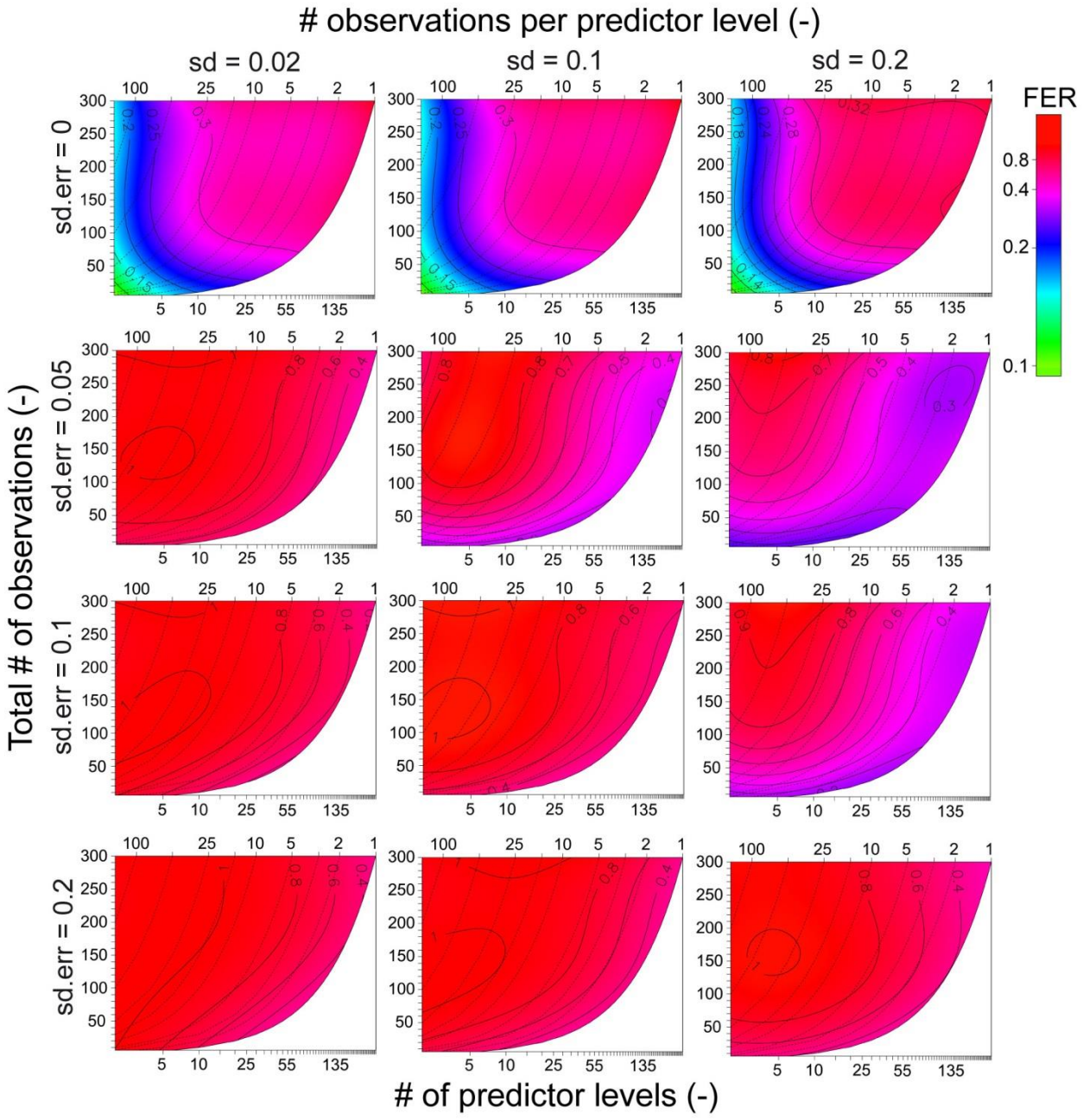
Appendix S1. Prediction success depicted as the precision of prediction (POP) for all five tested response patterns (A: no response, B: linear, C: exponential decay, D: unimodal centered, E: unimodal non-centered) and the average (F). POP values dependent on the total number of observations, number of predictor levels and number of observations per predictor level are depicted for an intermediate level of random variation (*sd* = 0.1) and no systematic error (*sd.err* = 0). The number of predictor levels is shown on the horizontal axis, the total number of observations on the y-axis; in consequence the number of observations per predictor level ("replicates") indicated on the scale at the upper margin follows the dashed isolines. The solid white isolines indicate areas with equal POP values.



Appendix S2. Prediction success depicted as the fraction of correctly detected response types (FCR, A ,C and E) as well as the precision of prediction (POP, B, D and F) for different levels of random variation of the response variable based on an average of the tested response patterns. FCR and POP values dependent on the total number of observations, number of predictor levels and number of observations per predictor level are depicted for *sd* = 2% (A and D), 10% (B and E) and 20% (C and F) of total variation (without a systematic error included, *sd.err* = 0). Solid lines show isolines for a selection of POP-values, dashed lines show isolines for a selection of number of observations per predictor level.



Appendix S3. Prediction success depicted as the fraction of correctly detected response types (FCR) for three different levels of random variation (*sd* = 2%, 10% and 20% of total variation) and four different levels of systematic error (*sd.err* = 0%, 5%, 10% and 20% of total variation) based on an average of the tested response patterns (without no-repsonse). FCR values dependent on the total number of observations, number of predictor levels and number of observations per predictor level are depicted. Solid lines show isolines for a selection of FCR-values, dashed lines show isolines for a selection of number of observations per predictor level.



Appendix S4. Probability of erroneous predictions depicted as the fraction of erroneous detected response types (FER) for three different levels of random variation (*sd* = 2%,10% and 20% of total variation) and four different levels of systematic error (*sd.err* = 0%, 5%, 10% and 20% of total variation) based on the no response pattern. The probability of erroneous pattern detection (0-1 equals 0 to 100%) dependent on the total number of observations, number of predictor levels and number of observations per predictor level are depicted. Solid lines show isolines for a selection of erroneous prediction probabilities, dashed lines show isolines for a selection of number of observations per predictor level.

Data S1. Simulation scripts for R.

```
######################################################################
### Optimizing sampling approaches along ecological gradients     ###
### by                                                            ###
### Andreas H. Schweiger, Severin D.H. Irl, Manuel J. Steinbauer, ###
### Juergen Dengler and Carl Beierkuhnlein                        ###
###                                                             ###
### Simulation script                                             ###
######################################################################

########################################
### Install and load required packages ###
########################################

#install.packages("caTools")
#install.packages("AICcmodavg")
#install.packages("multicore")
#install.packages("parallel")
require(caTools)
require(AICcmodavg)
#require(multicore) # requires a multiple core server with a Linux operating system, this
packages is out dated; therefore use the package 'parallel'
require(parallel)

########################################
### Functions used during the simulation ###
########################################

### Function to calculate whole number factorisations for n (number of replicates) based on each
tested N(total number of observations)

is.wholenumber <- function(x, tol = .Machine$double.eps^0.5)  abs(x - round(x)) < tol

### Function to find optimal model based on the sampled data. Function chooses from the five
considered  response shapes (no response as a null model/control, linear response, exponential
decay, unimodal response with centred maximum and unimodal response with non-centred maximum)
using the AICc (minimum)

optFit <- function(x,y){

  AICs <- rep(0,4)
  names(AICs) <- c("none","linear","exp","hump")
  test <- as.data.frame(cbind(y,x))
  colnames(test) <- c("y","x")

  AICs[1] <- AICc(lm(y~1)) # no pattern
  AICs[2] <- AICc(lm(y~x)) # linear-fit
  AICs[3] <- AICc(lm(y~exp(-x^0.3))) # exponential-fit
  AICs[4] <- AICc(lm(y~I(x^2)+x)) # unimodal-fit

  AICs[which(AICs=="-Inf")] <- 1000 # necessary when AICc cannot be calculated when N is to small
for a model fit (e.g. N=2 for an unimodal fit for which at least 3 observations along the
gradient are needed for a model fit)
  which.min(AICs)
}

#####################################################################
### Define the five 'true' response shapes tested in our study ###
#####################################################################

x <-  seq(0,1000,1)

noreponse <- rep(0.5,length(x)) # no reponse
linear <- function(x,a=-0.001,c=1){a*x+c} # linear
exponential <- function(x,a=0.3){exp(-x^a)} # exponential
unimodCentr <- function(x,a=-4.0e-6,b=4.0e-03){a*I(x^2)+b*x} # unimodal with centered maximum
unimodNonCent <- function(x,a=-1.0e-06,c=1){a*I(x^2)+c} # unimodal with non-centered maximum

func <- c("~1","~gradient1","~exp(-gradient1^0.3)","~gradient1+I(gradient1^2)") # function-
argument used in the sampling and evaluation algorithm
```

```
#########################################################################
### Define total sample size, systematic and random error for sampling ###
#########################################################################

sampl <- c(6,seq(10,300,10)) # total sample size N (6 to 300)
sd.err <- c(0,0.02,0.05,0.1,0.15,0.2,0.25) ## systematic error sd.err (0 to 25% of total
variation)
sds <- c(0.02,0.05,0.1,0.15,0.2,0.25) ## random error sd (0 to 25% of total variation)
setting.grid<-expand.grid(sampl,sd.err,sds)
colnames(setting.grid) <- c("smplsize","sd.err","sds")

head(setting.grid)

#########################################################
### Sampling and evaluation algorithm to parallelize ###
### simulations on a multiple core server            ###
#########################################################

ModEval <- function(smplsize,sd.err,sds){

  iter <- 1000 # number of iterations

  repRaw <-seq(1,(smplsize/2),1)
  repli <- repRaw[which(is.wholenumber(smplsize/repRaw))]## calculates whole number observations
per predictor level for each N
  sampl.points <- smplsize/repli # number of predictor levels (l) along the gradient

  Sim1 <- matrix(0,iter,length(repli)) # Matrix for results of the 'correct model' approach
  Sim2 <- matrix(0,iter,length(repli)) # Matrix for results of the 'precission of prediction'
approach
  colnames(Sim1) <- paste("Ap1",repli,sep="_")
  colnames(Sim2) <- paste("Ap2",repli,sep="_")

    for(k in 1:length(repli)){

    gradient <- seq(0,1000,length.out=sampl.points[k])

    syst.err <- rnorm(n=length(gradient),mean=0,sd=sd.err) ## generate a systematic error arround
the 'true' expectancy values
    y_true <-  linear(gradient)+syst.err ## 'true response ## `!!! here to vary the 'true'
response shape to be tested choosing from the commands: noreponse(),
linear(),exponential(),unimodCentr() or unimodNonCent()

    for(j in 1:iter){

      y_sim <- matrix(NA,repli[k],length(gradient))

      for(i in 1: length(gradient)){

        y_sim[,i] <- rnorm(n=repli[k],mean=y_true[i],sd = sds)## sampled response
      }

      gradient1 <-  rep(gradient,each=repli[k]) # underlying gradient to test the sampled
response

      ### first approach: correct model approach

      Modelselc <- as.numeric(optFit(gradient1,c(as.numeric(y_sim) , recursive = TRUE))) #
selecting the best model out of the five response shapes to choose from based on the sampled
response
      Sim1[j,k] <- Modelselc

      ### second approach: precsission of prediction approach

      modpred <- lm(as.formula(paste("c(y_sim , recursive = TRUE)",func[Modelselc],sep=""))) #
model chosen from model selection based on sampled response
      gradientTest <- data.frame(gradient1 = seq(0,1000,10)) # set a gradient for the predictor
variable to compare the predicted response based on the selected model to the 'true' response
```

```
      resp_pred <- predict(modpred,newdata=gradientTest) # predict the response based on the
model selection
      resp_true <- linear(gradientTest) ### predict the 'true' response for the same locations
along the gradient,  !!! here to vary the 'true' response shape to be tested choosing from the
commands: noreponse(), linear(),exponential(),unimodCentr() or unimodNonCent()

      Sim2[j,k] <- sum(abs(resp_true-resp_pred))/length(gradientTest[,1]) # calculate  how much
the inferred response shape deviated from the actual response shape
      Sim <- cbind(Sim1,Sim2) # write the results from the two different evaluation approaches
for each combination of N, sd.err and sd in the same element of a list object

      }
  }
  Sim # return list object
  }


############################################################
### Run simulations for the particular response shape on ###
### a multiple core server with a Linux operating system ###
############################################################

set.seed(10) # set random generator to set.seed(10) to get similar results

ModEvalLin <-
mcmapply(FUN=ModEval,smplsize=setting.grid[,1],sd.err=setting.grid[,2],sds=setting.grid[,3],mc.co
res=22,USE.NAMES=TRUE) # command to run the run parallel computations for all combinations of
N,l(n), sd.err and sd; When using the 'parallel' package (necessary in newer version of R as the
mclapply command is now implemented in the R-environment) you have to set SIMPLIFY = FALSE to get
a list object

save(ModEvalLin,file="ModEvalLin.RData") # save the results for one of the five tested response
shapes an r-object which can be used for the subsequent analyses
```

6 Summary

Springs are semi-aquatic ecosystems where micro-environmental conditions affecting the compositions of inhabiting plant species on local scale are strongly linked to the macro-environmental conditions of the surrounding landscape. This environmental and ecological coherence of springs provides experiment-like conditions to test fundamental ecological theories about the functioning of natural ecosystems. Despite their model character, springs are completely underrepresented in ecological research and empirical tests of general ecological theories are missing so far.

This thesis, which includes six manuscripts, aims to contribute to an integrative understanding of complex ecosystem functioning by combining long-term empirical research conducted on springs with theoretical, community and system ecological considerations. By combining recent and past investigations on water characteristics and plant community composition of seepage springs in the lower mountain regions of Central Germany, the long-term dataset used in this thesis documents long-term ecological responses to historic and emerging anthropogenic stressors over the last 25 years.

The theory of complex adaptive systems was used as a general theoretical framework for this thesis. This general theory defines ecosystems as a collectivity of biotic elements adaptively interacting with each other and the abiotic environment on varying spatial and temporal scales. Thus, five major principles qualify complex adaptive ecosystems: 1) diversity and organisation of system elements (i.e. species, communities), 2) flow, distribution and interaction of information, energy and matter in the ecosystem, 3) stability of ecological responses, 4) scale-dependence and cross-scale similarity of ecological processes and patterns and, 5) path-dependence and ecological memory of the ecological system. All five major principles were investigated empirically by at least one manuscript of this thesis.

While studying the diversity and organisation of plant communities inhabiting the investigated springs, three hyper-dominant (oligarchic) species were detected, which reflect the acidity and water temperature regime of the springs as major abiotic drivers of plant community composition. Springs that were less affected by historic acidification during the 20th century were characterised by the herb *Chrysosplenium oppositifolium* whereas antropogenically acidified springs were characterised by *Sphagnum* moss species. The grass species *Calamagrostis villosa* was characteristic for the cooler springs in the higher elevations of the study region. Spring plant communities that were less affected by historic acidification showed significantly higher stability to the climatic extreme summer of 2003 than strongly acidified springs. This alternative state in the plant community composition of anthropogenically acidified springs turned out to be further stabilised by positive feedbacks between historic acidification and biogenic habitat modification caused by *Sphagnum* species, which significantly affected long-term trajectories of plant community composition. These positive feedbacks as well as the interactive effects of abiotic conditions, which turned out to influence spring plant communities on varying temporal scales, stress the importance of path-dependence, abiotic-biotic interactions and ecological memory in these ecosystems. Furthermore, high cross-scale similarity was observed for the realised temperature niches of plant species inhabiting these springs. As cross-scale similarity is just rarely reported in current literature, I argue, that low environmental noise at local scale and strong cross-scale links between micro- and

macro-environmental conditions, both environmental characteristics of the studied springs, can explain this exceptional observation. Besides the empirical research presented here in the framework of a general ecological theory, methodical requirements to test and further develop ecological theories are discussed. Simulations based on artificial data show that the risk of statistical biases and, thus, misinterpretations of ecological patterns strongly varies with the amount and type of noise (random vs. systematic).

This thesis provides one of the first rigorous tests of the complex adaptive systems theory for natural ecosystems and fills numerous knowledge gaps about the structure and functioning of springs. Several fascinating research questions emerged from this dissertation, including the role of contingency and cross-scale interactions in explaining ecological patterns and processes. In general, the theory of complex adaptive systems is a promising candidate for a general theory of ecology with the potential to increase our understanding about the functioning of complex natural ecosystems.

7 Zusammenfassung

Quellen sind semi-aquatische Ökosysteme, in denen kleinskalige Umweltbedingungen, welche die Zusammensetzung der Pflanzengemeinschaften auf lokaler Ebene beeinflussen, stark mit den großskaligen Umweltbedingungen der umgebenden Landschaft verknüpft sind. Diese starke Kohärenz bietet experimentale Bedingungen um ökologische Theorien zur Funktionsweise von Ökosystemen zu überprüfen. Trotz ihres Modellcharakters sind Quellen in der ökologischen Forschung unterrepräsentiert und empirische Ansätze zur Überprüfung von generellen ökologischen Theorien fehlen gänzlich.

Das Ziel dieser Dissertation, die insgesamt sechs Manuskripte umfasst, ist es das Verständnis um komplexe Ökosystemfunktionen über die Kombination von gemeinschafts- und ökosystem-ökologischen Ansätzen zu erhöhen. Die hierzu genutzte Datengrundlage umfasst aktuelle sowie vergangene Geländeerhebungen zu Quellwassercharakteristika und der Pflanzenartenzusammensetzung von helokrenen Waldquellen der deutschen Mittelgebirge. Dieser Langzeitdatensatz dokumentiert hierbei ökologische Reaktionen auf historische und rezente Umweltveränderungen über die letzten 25 Jahre.

Den theoretischen Rahmen dieser Arbeit bildet die Theorie von komplexen adaptiven Systemen, die Ökosysteme als Kollektive biotischer Elemente definiert, welche sowohl untereinander also auch mit der abiotischen Umwelt auf unterschiedlichen räumlichen und zeitlichen Skalen miteinander in adaptiver Weise interagieren. Fünf theoretische Hauptprinzipien werden identifiziert, die empirisch für Quellen als Modellökosysteme betrachtet werden: 1) Diversität und Organisation von Systemelementen (Arten, Artgemeinschaften), 2) Fluss, Verteilung und Interaktion von Information, Energie und Materie im System, 3) Stabilität ökologischer Reaktionen, 4) Skalenabhängigkeit und skalenübergreifende Ähnlichkeiten von ökologischen Mustern und Prozessen und 5) Pfadabhängigkeit und ökologisches Gedächtnis von Ökosystemen.

Studien zur Diversität und Organisation der Quellpflanzengemeinschaften stellten drei hyper-dominante Arten heraus, welche das Aziditäts- und Temperaturregime der untersuchten Quellen signifikant widerspiegeln und drei Artgemeinschaften klar voneinander abgrenzen. Die nur wenig von der Jahrzehnte zurückliegenden, anthropogenen Versauerung beeinflussten Quellen werden hierbei von *Chrysosplenium oppositifolium* charakterisiert, während stark versauerte Quellen maßgeblich von *Sphagnum*-Moosen geprägt werden. Kühlere Quellen der Hochlagen werden durch *Calamagrostis villosa* charakterisiert. Die gering beeinflussten Quellgemeinschaften wiesen darüber hinaus eine sichtbar höhere Stabilität gegenüber dem klimatisch extremen Sommer 2003 auf als die deutlich durch Versauerung geschwächten Artgemeinschaften. In weiteren Studien zeigte sich, dass positive Rückkoppelungen zwischen historischer Versauerung und der biogenen Habitatmodifikation durch *Sphagnum*-Moose sich signifikant auf die Langzeitveränderungen der Quellartenzusammensetzung auswirken und somit den alternative Zustand der stark versauerten Quellen über Jahrzehnte hinweg stabilisieren können. Diese Beobachtungen verdeutlichen die signifikante Rolle von abiotisch-biotischen Interaktionen und des ökologischen Gedächtnisses dieser Ökosysteme. Darüber hinaus ließen sich starke skalenübergreifende Ähnlichkeiten in den realisierten Temperaturnischen der quellbewohnenden Pflanzenarten nachweisen, was im Gegensatz zu den meisten Beobachtung zur Skalenabhängigkeit von ökologischen Mustern und

Prozessen steht. Als Erklärung hierfür diskutiere ich die Effekte von lokal konstanten Umweltbedingungen und starken skalenübergreifenden Verknüpfungen von mikro- und makroklimatischen Faktoren, beides Merkmale der untersuchten Quellen, auf das Auftreten von Skalenabhängigkeit ökologischer Muster. Neben den empirischen Betrachtungen umrahmen methodische Überlegungen zur Erhebung ökologischer Daten diese Dissertation, wie sie zum Testen und Fortentwickeln von ökologischen Theorien unabdinglich sind. Simulationen basierend auf künstlichen Daten zeigen, dass das Risiko statistisch basierter Fehlinterpretationen ökologischer Muster stark durch Ausmaß und Art des Umweltrauschens beeinflusst wird.

Durch eine der ersten umfassenden Überprüfungen der Theorie von komplexen adaptiven Systemen für natürliche Ökosysteme schließt diese Dissertation nicht nur bestehende Lücken im mangelnden, ökologischen Wissen um Quellen, sondern bietet darüber hinaus umfassende übertragbare Einblicke in die Funktionsweise natürlicher Ökosysteme. Darauf basierend ergeben sich spannende weiterführende Fragestellungen, unter anderem zur Rolle von Zufall und skalenübergreifender ökologischer Interaktionen auf die Ausprägung und den Nachweis ökologischer Muster und Prozesse. In der Zusammenschau bietet die Theorie von komplexen adaptiven Systemen die Grundlage für eine generelle ökologische Theorie, die unser Verständnis um die Funktionsweise von natürlichen Ökosystemen deutlich bereichern kann.

8 Acknowledgements

Life is full of decisions you have to make. And most of the time you are not sure whether the decision you made was right or wrong. However, when I decided to go back to university to study ecology after finishing my studies in environmental engineering, I was quite sure that this is the right way to go. Numerous people encouraged me to do that and I want to thank these people although I do not name all of them in the following lines.

First of all I want to thank Heiner Schöpf, the former head of the Bavarian ornithological institute, who unfortunately passed away too young but dedicated his entire life to protect nature. Thank you Heiner for your endless passion for nature that made a lasting impression on me. Secondly, I want to thank Dr. Peter Miotk, one of the last 'old ecologists', a 'lover of butterflies and birds' and everything else which lives out there in nature. He further stimulated my passion for ecology as a scientific discipline.

I want to especially thank Prof. Dr. Carl Beierkuhnlein for giving me scientific guidance and the freedom to work on numerous, fascinating facets of ecology and biogeography the last three years. Besides his excellent scientific skills I especially enjoyed his holistic perspectives on the complexity of nature.

Furthermore I thank the renowned Island Boy Group (David, Manuel and Severin) for numerous, very intensive discussions related to ecological but also any other topics. Special thanks go to Severin as my office colleague, a sometimes quite challenging exercise.

I also want to thank Julienne Schiebold for her help, advice, love and support during the last years and hopefully during the years to come as well.

Above all, I want to thank my parents for supporting me with my ideas during my entire life until now.

Finally, I thank nature for being complex, a fact that makes ecology for me the most challenging but at the same time most fascinating discipline of natural science. After three years of working on various problems in ecology, I still think that this discipline of science is the right track for me to pursue.

9 Appendix

Appendix 1: Additional conference contributions to other topics during the time of my dissertation where I was the presenting author.

Date	Organisation	Conference and location	Title	Type
10/2013	Deutsche Ornithologen-Gesellschaft (DO-G)	146th Annual Meeting, Regensburg, Germany	Bayerische Steinadler als Nahrungsgeneralisten am nördlichen Alpenrand	Oral, invited
03/2014	Ecological Society of Germany, Autria and Switzerland (GfÖ)	8th Annual Meeting of the Specialist Group of Macroecology, Halle (Saale), Germany	Optimal-sized prey availability shapes global distribution patterns of the Golden Eagle Aquila chrysaetos	Oral
03/2014	Ornithologische Gesellschaft in Bayern	4th Annual Meeting, Benediktbeuren, Germany	Bayerische Steinadler als Nahrungsgeneralisten am Alpenrand	Oral, invited
01/2015	International Biogeography Society (IBS)	7th International Conference, Bayreuth, Germany	Advantages on the dark side of insect coloration	Poster
06/2015	British Ecological Society (BES), GfÖ et al.	EU Macro 2015, Copenhagen, Denmark	Prey size affects reproductive success and global distribution of the Golden Eagle	Poster

Appendix 2: Additional manuscripts to other topics which arose during the time of my dissertation (only published articles).

Schweiger AH, Fünfstück H-J, Beierkuhnlein C (2013) Bayerische Steinadler als Nahrungsgeneralisten am nördlichen Alpenrand. *Vogelwarte: Zeitschrift für Vogelkunde* **51(4)**, 296-298.

Schweiger AH, Fünfstück H-J (2014) In der Not frisst der Steinadler alles (außer Fliegen). *Der Falke: Journal für Vogelbeobachter* **7**, 38-40.

Schweiger AH, Otieno DO, Kulunge SR, Reineking B, Tenhunen J (2015) The Afro-alpine dwarf shrub Helichrysum citrispinum favours understorey plants through microclimate amelioration. *Plant Ecology and Diversity* **8(3)**, 293-303.

Schweiger AH, Fünfstück H-J, Beierkuhnlein C (2015) Availability of optimal-sized prey affects global distribution patterns of the golden eagle Aquila chrysaetos. *Journal of Avian Biology* **46(1)**, 81-88.

Schweiger AH, Beierkuhnlein C (2015) Size dependency in colour patterns of Western Palearctic carabids. *Ecography* (2015), doi: 10.1111/ecog.01570.

Steinbauer MJ, Schweiger AH, Irl SDH (2016) Patterns in Biogeography. In: Encyclopedia of Evolutionary Biology (ed Kliman R) vol. 1, pp. 221-230, Elsevier Academic Press, Oxford, doi: 10.1016/B978-0-12-800049-6.00110-4.

10 Declarations

(Eidesstattliche) Versicherungen und Erklärungen

(§ 5 Nr. 4 PromO)

Hiermit erkläre ich, dass keine Tatsachen vorliegen, die mich nach den gesetzlichen Bestimmungen über die Führung akademischer Grade zur Führung eines Doktorgrades unwürdig erscheinen lassen.

(§ 8 S. 2 Nr. 5 PromO)

Hiermit erkläre ich mich damit einverstanden, dass die elektronische Fassung meiner Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung hinsichtlich der eigenständigen Anfertigung der Dissertation unterzogen werden kann.

(§ 8 S. 2 Nr. 7 PromO)

Hiermit erkläre ich eidesstattlich, dass ich die Dissertation selbständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe.

(§ 8 S. 2 Nr. 8 PromO)

Ich habe die Dissertation nicht bereits zur Erlangung eines akademischen Grades anderweitig eingereicht und habe auch nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden.

(§ 8 S. 2 Nr. 9 PromO)

Hiermit erkläre ich, dass ich keine Hilfe von gewerblichen Promotionsberatern bzw. -vermittlern in Anspruch genommen habe und auch künftig nicht nehmen werde.

…….

Ort, Datum, Unterschrift